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TASSEL-EARED SQUIRREL POPULATION DYNAMICS IN ARIZONA: INDEX TECHNIQUES AND RELATIONSHIPS TO HABITAT CONDITION

A Final Report

NORRIS L. DODD
STEVEN S. ROSENSTOCK
C. RICHARD MILLER
RAYMOND E. SCHWEINSBURG

September 1998

FEDERAL AID IN WILDLIFE
RESTORATION PROJECT

Arizona Game and Fish Department Mission

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Federal Aid in Wildlife Restoration
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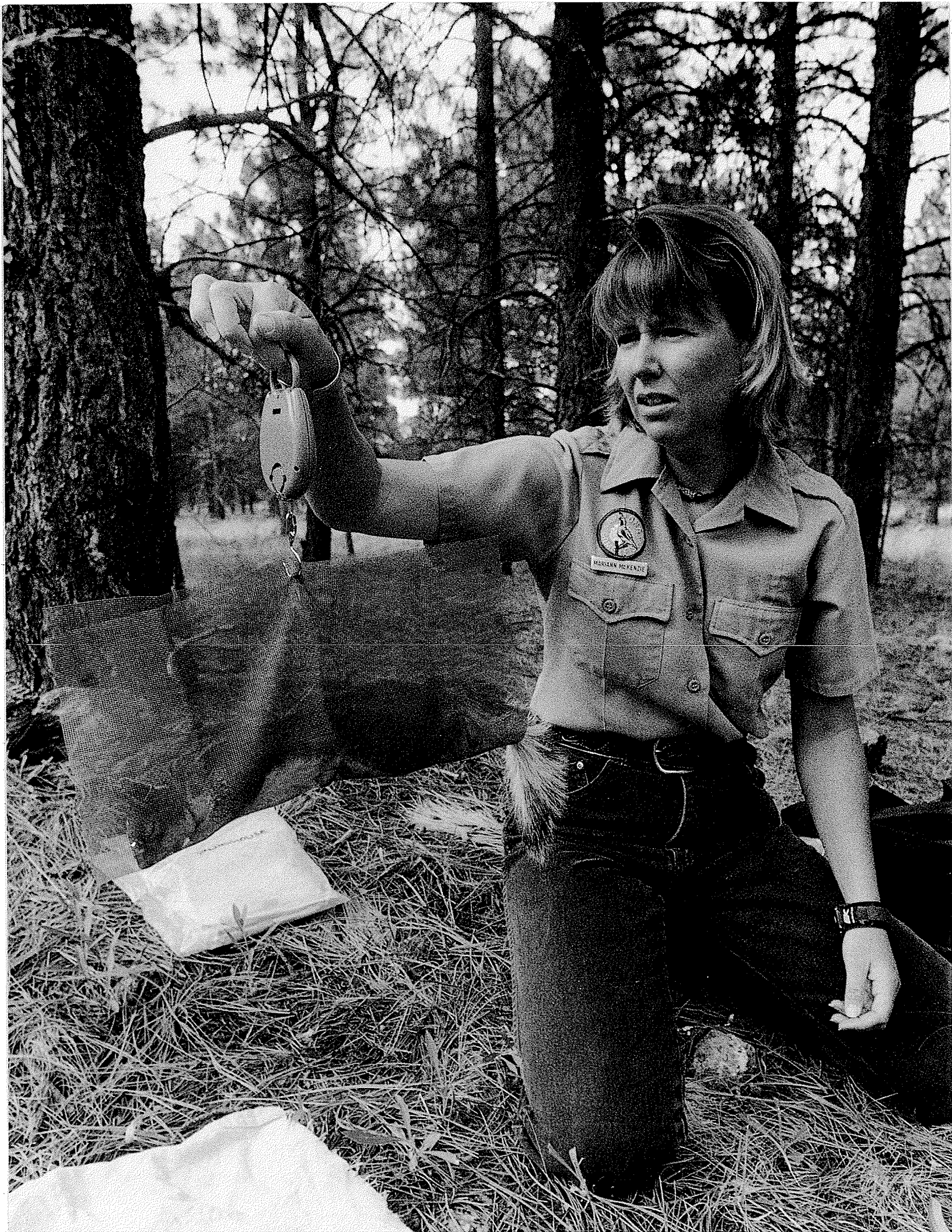
MARIANN MCKENZIE

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TASSEL-EARED SQUIRREL POPULATION DYNAMICS IN ARIZONA: INDEX TECHNIQUES AND RELATIONSHIPS TO HABITAT CONDITION

Norris L. Dodd, Steven S. Rosenstock,
C. Richard Miller, and Raymond E. Schweinsburg

Abstract: We examined seasonal tassel-eared squirrel (*Sciurus aberti*) population dynamics at 8 study sites in north-central Arizona during 1996-1997. This report describes our development of reliable squirrel density estimation techniques and relationships between population dynamics and structural habitat attributes. Study sites averaged 66 ha and exhibited considerable variation in habitat structure. We established 12 X 12 grids (70 m spacing) for trapping and sampling. To estimate squirrel populations, we conducted capture-recapture trapping twice during 3 seasons each year. We accrued 56,016 trap days and 2,542 captures of 450 individual squirrels (46% male, 54% female), and attained population estimates with mean standard error ±10.2%. Uncorrected (for squirrel home range edge effect) densities across all periods ranged from 0.05 to 1.03 squirrels/ha, with lowest mean density in January (0.25 squirrels/ha) and highest in August (0.44 squirrels/ha). Density fluctuated widely at half our study sites. However, edge effect-corrected densities were relatively stable across seasons ($\bar{x} = 0.16$ squirrels/ha). We attributed seasonal fluctuations in uncorrected squirrel density to food (pine seed from ovulate cones) availability, expanded seasonal home ranges, and immigration. Recruitment averaged only 0.14 juveniles/female and did not contribute to fluctuations in density. Survival rates averaged 0.78. The winter survival rate (0.63) was significantly lower than other periods, and survival during the fall period encompassing hunting season was 0.81. Regression analysis was used to assess relationships between squirrel density and track, feeding sign, and nest count indices. Spring feeding sign ($r^2 = 0.901$, $P < 0.001$) and track station ($r^2 = 0.925$, $P < 0.001$) density estimation techniques exhibited high precision, low type I and II error rates, and consistency among years and observers. None of the index techniques performed well during winter or summer/fall. Structural habitat variables were related to squirrel population variables by Spearman rank correlation analysis. Our strongest relationships were attained between interlocking canopy trees and squirrel recruitment ($r_s = 1.000$, $P < 0.001$), and basal area for all trees ($r_s = 0.919$, $P = 0.003$) and squirrel fitness (= density x survival x recruitment). Forest management practices that focus on intensive, widespread thinning will adversely impact tassel-eared squirrels. By integrating squirrel requirements for interlocking canopies, tree basal area, and other structural attributes in forest management plans, squirrel populations will be benefitted.

Key words: Arizona, basal area, density, forest management, habitat relationships, hunting impact, index techniques, *Pinus ponderosa*, ponderosa pine, population dynamics, recruitment, *Sciurus aberti*, survival, tassel-eared squirrels.

INTRODUCTION

The tassel-eared squirrel (*Sciurus aberti*) is an important small game species in Arizona, a popular watchable species, and a key prey species for the northern goshawk (*Accipiter gentilis*) (Reynolds et al. 1992). Squirrels play a key role in symbiotic nutrient and water exchange cycles within ponderosa pine (*Pinus ponderosa*) forests (States 1992, States and Wettstein 1998). Despite considerable research, questions about tassel-eared squirrel population dynamics remain at the center of issues involving forest management and sport hunting impact on squirrels and goshawks that rely on them for prey.

Timber harvest and even-aged forest management practices have intensified in Arizona since 1980 (Arizona Game and Fish Department 1990, 1993*a*; Johnson 1994). Such practices can reduce short-term canopy closure, tree density, large overstory trees, diversity, and patchiness. These practices are considered detrimental to tassel-eared squirrels (Pederson et al. 1976, 1987; Patton 1984; Patton et al. 1985; Arizona Game and Fish Department 1993*a*). Extensive and repeated even-aged timber harvest has led to cumulative effects to squirrel habitat (Dodd and Adams 1989, Arizona Game and Fish Department 1993*a*). Intensive timber harvest can also alter microhabitats where hypogeous fungi grow, reducing food for squirrels and potentially

disrupting the symbiotic relationship between fungi, pines, and squirrels (States 1985, Pederson et al. 1987, States et al. 1988, States and Gaud 1997). Adverse weather reduces tassel-eared squirrel populations (Keith 1965, Stephenson and Brown 1980), and reduced habitat quality coupled with diminished food quality and availability may exacerbate the effects of severe winters.

Timber harvest, long-term fire suppression, and livestock grazing have contributed to substantial changes in southwestern ponderosa pine forests since European settlement. Pre-settlement forests are thought to have been more open and park-like (Covington and Moore 1991, 1992, 1994; Belsky and Blumenthal 1997). Cooper (1960) stressed that although forests were more open then, considerable patchiness existed, with clumps of similar-aged trees interspersed throughout the landscape. Forests today support many more younger age class trees (Johnson 1994). Current forest conditions have increased the potential for catastrophic fire, disease, and decreased health of the ponderosa pine ecosystem (Covington and Moore 1991, 1992, 1994). These problems spawned forest health restoration initiatives (DellaSala et al. 1995). Such initiatives advocate aggressive thinning of forests to improve tree growth, increase the incidence of prescribed fire, and promote old-growth forest conditions (Covington and Moore 1992, 1994).

Concurrent with forest restoration initiatives, there has been increased attention to management of northern goshawk habitats (Reynolds et al. 1992). Goshawk management guidelines also promote aggressive thinning and opening of the forest on a landscape scale, particularly within foraging areas (Reynolds et al. 1992). There is concern that combined implementation of forest restoration and goshawk management guidelines, at a landscape scale, may degrade squirrel habitat.

Tassel-eared squirrels were hunted sporadically in Arizona from 1934 to 1953. Since then, hunting pressure has increased and squirrels have become popular small game. Annual tassel-eared squirrel harvest in Arizona increased from 15,337 in 1961 (Kufeld 1962) to 53,576 in 1971 (Brown 1972). Average annual squirrel harvest was 75,089 in 1979 to 1983 (Arizona Game and Fish Department 1986), increased to 122,575 from 1984 to 1988, and declined from 1989 through 1993 to 65,182 (Arizona Game and Fish Department 1993*b*). At the 1979 to 1983 harvest levels, there were no indications that tassel-eared squirrels were overharvested in Arizona (Brown 1984). Nevertheless, sport hunting impact on an important goshawk food source is unknown (Brown 1995). Although Brown (1984:94) discounted the impact of hunting on squirrel populations in Arizona, he concluded that "we still do not know what level of hunt pressure on tassel-eared squirrels causes hunt mortality to become additive to natural mortality."

The ability to address questions about the effects of habitat modification and sport hunting on tassel-eared squirrel populations has been limited by lack of a reliable, efficient population estimation technique. Since Kufeld's (1966) attempt to establish techniques for tree squirrel inventory met with limited success, no study has yielded a reliable means to estimate tassel-eared squirrel populations. Keith (1965) reported that ponderosa pine terminal branch clipping sign could be used to assess changes in squirrel abundance. Brown (1982) established a strong relationship between a clipping-count index and squirrel hunting success, but concluded that it was sensitive only to tracking gross tassel-eared squirrel population levels and trends. Keith (1965) suggested that the number of nests containing green material could be used as an indicator to tassel-eared squirrel abundance.

Pederson et al. (1976) and Patton and Wadleigh (1986) reported poor correlations between squirrel numbers and clippings, though the latter found a significant correlation 1 year in 7. Pederson et al. (1976) concluded that the incidence of clippings might reflect scarcity of other preferred foods rather than squirrel population levels. Gaud et al. (1993) found a strong inverse relationship between clippings and number of cones used by squirrels. In spite of the limitations, several studies used clipping counts as an index to tassel-eared squirrel numbers or density, including Ffolliott and Patton (1978), Hall (1981), and Ffolliott (1990). Several researchers pointed to the need to calibrate indices to known squirrel densities, including Patton (1974), Brown (1982), States et al. (1988), and Ffolliott (1990).

Development of population estimation techniques for eastern gray squirrels (*Sciurus carolinensus*) also has met with limited success in spite of greater effort expended than for tassel-eared squirrels. Few studies used known squirrel populations for technique calibration, and most successful efforts to census squirrels relied on labor intensive and costly direct sampling methods (Flyger 1959, Bouffard and Hein 1978).

Study Objectives

As a result of the above issues, a problem analysis was conducted to determine the need for additional research involving tassel-eared squirrels (Brown 1995). It allowed us to identify and prioritize 3 research needs: 1) evaluation of forest management practices at the landscape scale, 2) evaluation of sport hunting impact, and 3) development of a reliable and efficient population estimation technique (Brown 1995). Though other needs were considered higher priority, we concluded that if a reliable population estimation technique was developed, it could be the basis to address habitat and hunting related issues. Thus, we selected development of a population index technique as our primary goal. Specific objectives of our study were to:

- Estimate seasonal tassel-eared squirrel density, survival, and recruitment across study sites (Chapter I);
- Conduct index counts of squirrel nests, seasonal feeding sign, and tracks, and determine the strength and consistency of the relationships between seasonal squirrel density and index counts to evaluate their utility in estimating squirrel density (Chapter II);
- Quantify relationships between squirrel population dynamics and forest habitat structural characteristics (Chapter III); and
- Develop population index technique and forest management options which could enhance management of tassel-eared squirrels and their habitats.

Because of the complexity associated with reporting the methods, results, and discussion for these objectives, we have reported each of the first 3 objectives as a separate chapter.

STUDY AREAS

We conducted our study during 1996 and 1997 at 8 sites located in north-central Arizona (Fig. 1). We selected study sites crossing a wide gradient of forest structural conditions. Criteria for study site selection were: 1) homogeneous forest structural conditions ≥ 60 ha; 2) sites without substantial habitat modification at least 3 years prior to the study; and 3) logistical factors (e.g., access for winter squirrel trapping).

Seven of the 8 study sites were located on the Coconino and 1 on the Kaibab national forests. All sites were within the ponderosa pine association of the montane coniferous forest community (Brown 1994) and within the range of the Abert squirrel (*S. a. aberti*). All sites were subject to squirrel hunting and livestock grazing. Study sites and their general forest structural conditions were:

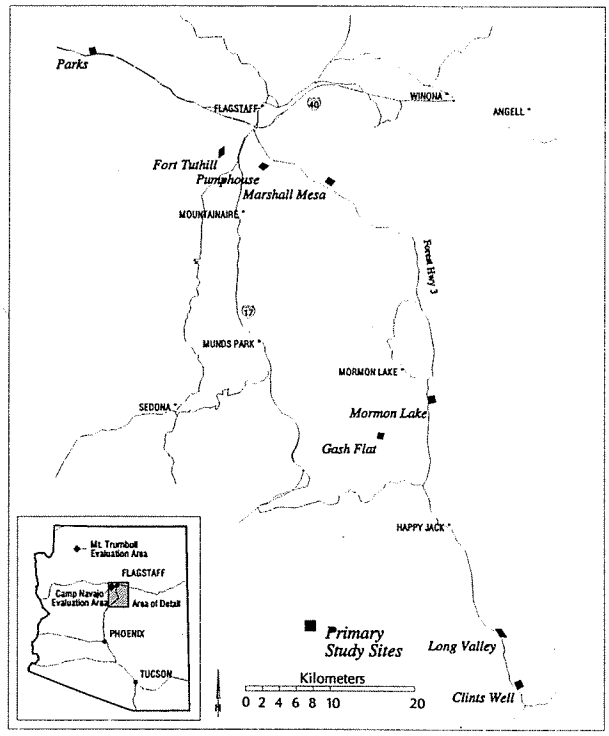


Figure 1. Location of 8 primary tassel-eared squirrel research study sites, and 2 population index technique evaluation areas (map inset) studied 1996-97. Shaded area on map inset corresponds to detailed map of primary study sites.

(a) Clints Well

(b) Ft. Tuthill

(c) Gash Flat

(d) Long Valley

Figure 2. Characteristic stand overviews of tassel-eared squirrel research study sites.

Clints Well. The Clints Well site was 70 km southeast of Flagstaff, at 2,100 m elevation (Fig. 2a). The site was predominately (>80%) unlogged uneven-aged forest dominated by clumps of large [>70 cm diameter at breast height (dbh)] old growth ponderosa pine. It supported a dense, clumped understory of sapling (4-12 cm dbh) and pole-sized (13-30 cm dbh) ponderosa pine. Basal area averaged 39.8 m^2/ha. The southern 20% of the site had been selectively logged in 1985, but retained old growth characteristics.

Ft. Tuthill. The Ft. Tuthill site was 5 km southwest of Flagstaff, at 2,180 m elevation (Fig. 2b). It was an even-aged site dominated by an overstory of small sawtimber-sized (30-45 cm dbh) ponderosa pine and scattered Gambel oak (*Quercus gambelii*), with a shrub understory of New Mexican locust (*Robinia neomexicana*). Mean basal area was 16.2 m^2/ha. It abutted dense, uneven-aged forest on 2 sides, thereby exhibiting a marked edge effect. The study area was last logged in 1992 by heavy commercial thinning and overstory removal.

Gash Flat. Gash Flat was 37 km southeast of Flagstaff at 2,225-2,260 m elevation (Fig. 2c). It was characterized as an even-aged stand dominated by sawtimber-sized (20-40 cm dbh) ponderosa pine, with sparse Gambel oak overstory. Mean basal area was 22.1 m^2/ha. The surrounding forest was structurally similar. This site was last logged in 1982 by commercial thinning. This area received more snow than other areas and was inaccessible during winter and spring 1997.

Long Valley. Long Valley was 60 km southeast of Flagstaff, at 2,075 m elevation (Fig. 2d). The site was heavily logged in 1982 and was dominated by small sawtimber-sized (20-35 cm dbh) ponderosa pine, with sparse Gambel oak. It was very open with remaining trees occurring in well-defined clumps, with a mean basal area of 16.8 m^2/ha. The surrounding forest was structurally similar, though not as open or clumpy. The "Pot Fire" burned approximately half the area in June 1996.

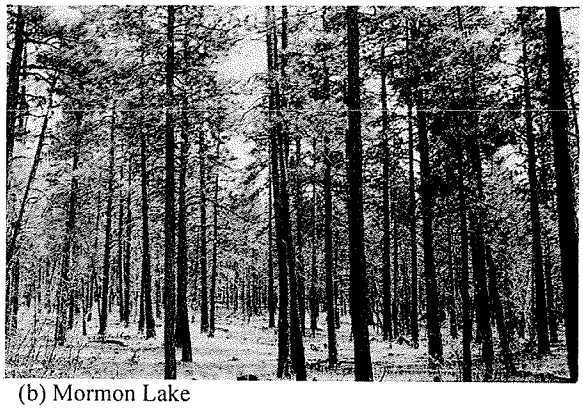
Marshall Mesa. Marshall Mesa was 10 km east of Flagstaff, on the rim of Anderson Mesa, at 2,195 m elevation (Fig. 3a). It was a diverse, uneven-aged site characterized by clumps of large (>60 cm dbh) ponderosa pine scattered among dense small sawtimber (30-40 cm dbh). Basal area averaged 31.7 m^2/ha. Gambel oak and junipers (*Juniperus* spp.) occurred throughout the site. The site was surrounded by forest of similar structural condition. It was last selectively cut by railroad logging during 1919 to 1920.

Mormon Lake. The Mormon Lake site ranged from 2,285-2,375 m in elevation and was located 35 km southeast of Flagstaff (Fig. 3b). Its small sawtimber-sized (30-40 cm dbh) ponderosa pine overstory was generally even-aged and well spaced. Basal area averaged 24.8 m^2/ha. Sparse Gambel oak occurred throughout the site. Forest of similar condition occurred on 3 sides, with denser, mixed-conifer forest on 1 side. Pulpwood (20-30 cm dbh) harvest occurred at Mormon Lake during 1991. This site received and held more snow than other study areas.

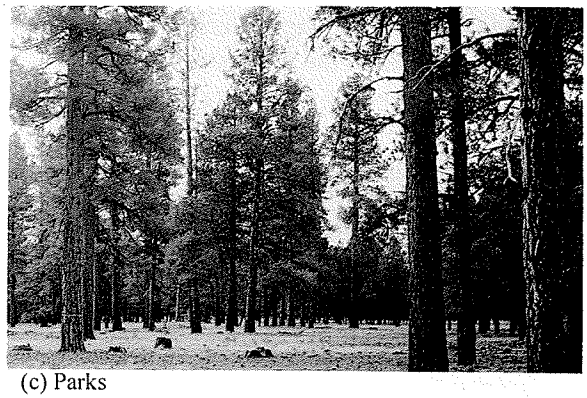
Parks. Parks was located on the Kaibab National Forest, 20 km west of Flagstaff at 2,165 m elevation (Fig. 3c). It contained many open clumps of large (>65 cm dbh) old growth ponderosa pine, and approximated "pre-settlement" forest conditions (Cooper 1960, Covington and Moore 1994). Clumps of pole (12-30 cm dbh) and small sawtimber-sized (30-40 cm dbh) pine also occurred throughout the area. Mean basal area was 26.8 m^2/ha. Denser forest conditions occurred adjacent to the study site. Past logging was selective, and approximately 20% of the area was lightly and irregularly thinned in 1995, resulting in minimal change to existing stand character.

Pumphouse. The Pumphouse site was 2 km south of Flagstaff, at 2,150 m elevation (Fig. 3d). It was vegetated by open, immature (30-40 cm dbh) and mature (41-50 cm dbh) sawtimber-sized ponderosa pine, which occurred in clumps. Only sparse, scattered remnants of the larger (>50 cm dbh) overstory tree component remained after past logging. Basal area averaged 18.2 m^2/ha. The most recent harvest was a commercial thinning in 1985.

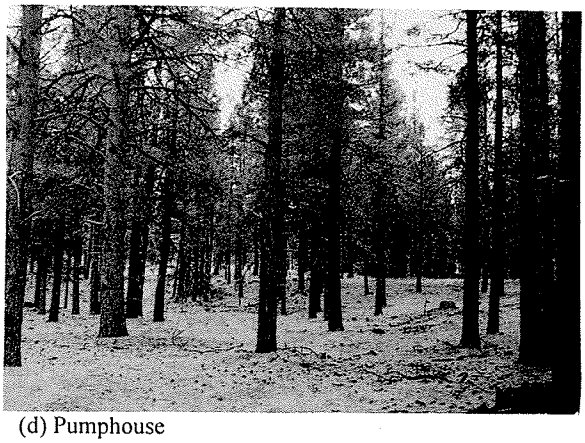
(a) Marshall Mesa



(b) Mormon Lake



(c) Parks



(d) Pumphouse

Figure 3. Characteristic stand overviews of tassel-eared squirrel research study sites.

In addition to 8 primary study sites, squirrel population indices were evaluated at ongoing forest restoration evaluation study areas at Camp Navajo (Rosenstock et al. 1997) and Mount Trumbull (Germaine 1997) (Fig. 1). Three sites inhabited by Abert squirrels were used to evaluate index techniques at Camp Navajo, 25 km west of Flagstaff. All 3 sites were generally uneven-aged and clumpy, though the large tree overstory was reduced by past timber harvest. Gambel oak was prevalent, along with scattered junipers. Study sites were not grazed by livestock during the past 3-5 years, and infrequent squirrel hunting occurred by military personnel.

The Mount Trumbull area was located 170 km northwest of Flagstaff (Fig. 1). The area's Kaibab squirrel (*S. a. kaibensis*) population was established by transplants from 1972 to 1977 (Brown 1984). Six sites were used to evaluate population index techniques. They ranged from uneven-aged forest with scattered large (>60 cm dbh) overstory ponderosa pine to predominately even-aged sites dominated by sawtimber-sized (30-45 cm dbh) ponderosa pine. Gambel oak and New Mexican locust were overstory components and also dominated the understory with big sagebrush (*Artemisia tridentata*). Forests on Mount Trumbull have been subjected to timber harvest, though logging in the past 20 years has only been associated with current forest restoration activities (Covington and Fule 1995). Evaluation sites were subject to livestock grazing and squirrel hunting.

Weather during the project at the primary study area (National Weather Service; Bellemont, Ariz.) was generally dry: 1995 was the 17th driest year on record (39.9 cm versus 57.9 cm mean precipitation), 1996 the 4th driest (30.0 cm), and 1997 the 7th driest (35.1 cm). Temperatures typically were normal except that winter 1995-1996 was warmer than normal.

Snowfall during winter 1995 totaled 85.6 cm (8th lowest on record; $\bar{x}$ = 242.8 cm). Only 5 snow "events" occurred with accumulations ≥ 10 cm (depth at which squirrel mortality occurs; Stephenson and Brown 1980), and there were only 12-21 days with snow depth ≥ 10 cm on the 8 study sites. Winter 1996-1997 was dramatically different, and in spite of the overall dry conditions, snowfall was the 13th highest on record (338.3 cm), with 9 events depositing ≥ 10 cm. Total duration of snow depth of ≥ 10 cm on the study sites was 61-74 days.

CHAPTER I

SEASONAL TASSEL-EARED SQUIRREL POPULATION DYNAMICS

METHODS

Capture-Recapture Trapping

We employed capture-recapture techniques to obtain squirrel population estimates (Pollock et al. 1990, Otis et al. 1978). Following recommendations in White et al. (1982) for optimizing plot design and layout, we established 12 X 12 trapping grids with 70 m spacing (Fig. 4). Trap points were marked with numbered aluminum tags. Our target grid size was 60 ha, but actual size varied as a result of topography, habitat heterogeneity, and other factors. We used differentially corrected Global Positioning System (GPS) data to calculate accurate grid size for each study site.

We trapped during 3 periods each year in January (post-hunt/early winter), April (post-winter/pre-breeding) and August (pre-hunt/post-breeding) during 1996-1997. We used Tomahawk® No. 202 (Tomahawk Live Trap Co.) traps baited with 15-25 unsalted raw or roasted, unshelled peanuts (Patton et al. 1976). Trapping periods were 8-12 days, contingent on attaining population estimates with standard errors below ±10%. Study sites were trapped simultaneously. During January and April, traps were set and baited early morning and checked and closed at dark. In August, traps were open continuously and checked twice a day, mid-morning and at dark.

Captured squirrels were immobilized using Metofane® (Pitman-Moore) (Patton et al. 1976, Pederson et al. 1987). A numbered metal ear tag (Monel No. 3; National Band and Tag Co.) and colored plastic collar were affixed to each squirrel. We visually determined sex and obtained body weights with a 1,000 g spring scale to the nearest 5 g. We relied on differential body weight and morphological characteristics to separate juvenile from adult cohorts (Farentinos

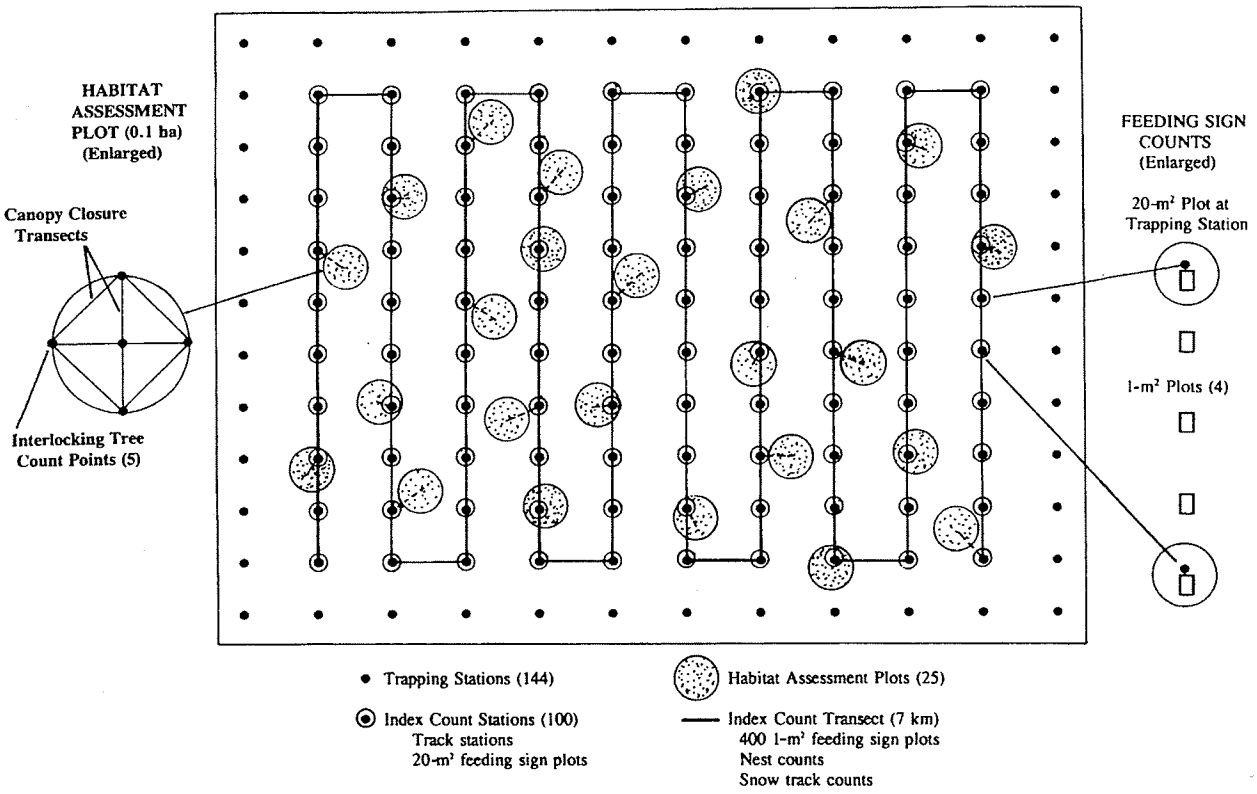


Figure 4. Layout of 8 north-central Arizona tassel-eared squirrel study sites, including trapping stations and transects, and habitat assessment plots.

1972*a*, Keith 1965). Squirrels were released at the capture site upon recovery (15-20 min). We also recorded numbers of "non-target" species caught and released at each site.

Trapping was also conducted in March 1997 immediately adjacent to the Ft. Tuthill study area to assess seasonal population fluctuations and winter movement patterns. We established 12 lines, 70 m apart, and placed traps along each line at the edge and outward at 70, 175, 280, and 385 m (60 total). Trapping was conducted for 5 days and the presence and location of marked squirrels was recorded to determine the distance they moved into adjacent habitat.

Population Variable Estimation

Population and Density. We computed population estimates using the program CAPTURE (White et al. 1982, Rexstad and Burnham 1991). We used this program to test population closure assumptions and behavioral response of squirrels to capture. The program then selected appropriate estimation models for each data set that minimized capture-related sources of variation in capture probabilities. The selected model was used to derive population estimates, standard errors, and 95% confidence intervals.

"Uncorrected" squirrel densities (= "naive" density; Otis et al. 1978, White et al. 1982) were calculated by dividing population estimates by the size of each study area. These density estimates did not account for squirrel edge effect influences, primarily related to squirrel home ranges that only partly overlapped onto trapping grids. "Corrected" densities were computed by the same program CAPTURE models used to derive population estimates. We used 4 nested grids to correct for the influence of edge effect. Program CAPTURE jointly estimated corrected density and an effective area boundary strip width around each nested grid by applying a nonlinear least-squares procedure (Otis et al. 1978, White et al. 1982).

Survival Rates. To estimate squirrel survival between trapping periods, we used the "robust design" (Pollock 1982, Pollock et al. 1990). It combined pooled closed population capture-recapture histories and the open population Jolly-Seber model. Survival rates (non-juvenile) and standard errors were derived for intervals between trapping efforts using the program JOLLY (Jolly 1965, Pollock et al. 1990).

Recruitment. The emergence of juveniles from maternal nests generally occurs in August (Brown 1984). Our August trapping periods occurred too early to reliably capture juveniles following their emergence from maternal nests. Therefore, we used the number of juvenile squirrels caught during our January trapping periods to estimate recruitment for each study site, measured as juveniles/adult female (Brown 1984).

Fitness. Van Horne (1983) proposed a measure of fitness relating to habitat quality using density, mean individual survival probability, and mean offspring production. Squirrel fitness for our study sites was estimated from the product of mean corrected density, recruitment, and survival.

Statistical Analyses

All statistical tests were performed using the program STATISTICA® (Statsoft, Inc. 1994). Results of all statistical tests were considered significant at $P \leq 0.05$. Mean values are reported with ± standard errors.

We assessed differences in squirrel population estimates among study areas and among trapping periods using 95% confidence intervals derived from program CAPTURE. Differences were considered significant if confidence intervals did not overlap.

We used analysis of covariance (ANCOVA) to assess differences in mean squirrel density, survival rates, and recruitment among periods, removing the influence of study site effects from the comparisons (Hays 1981). For significant ANCOVAs, we assessed pairwise differences between periods with Sheffe's multiple comparison test; this procedure was considered conservative (Hays 1981, Statsoft, Inc. 1994). We also used ANCOVA and Sheffe's test to assess differences in non-target species captures among periods following square root transformation of these count data (Steel and Torrie 1980). For the squirrel trapping conducted in March 1997 adjacent to Ft. Tuthill, we used a Chi-square 2 X 2 table to test for differences in frequencies of capture of marked and unmarked squirrels 0-175 m and >175 m from the study site edge.

RESULTS

Capture-Recapture Trapping

A total of 56,016 trap days accounted for 2,542 squirrel captures (Table 1). An average of 8.5 days of trapping was required to achieve our target standard errors associated with population estimates. Exceptions included August 1996, when trapping was halted earlier at 3 study sites when northern goshawks harassed trapped squirrels, and in January 1997 when heavy snows ended trapping after 5 days. Trapping effort declined from 60.3 trap days/capture in January 1996, to 14.2 trap days/capture in April 1997; across all periods, 22.0 trap days were required per capture.

Trapping mortality averaged 1.3% (±0.2) during our study (Table 1); nearly 60% of mortalities (22) occurred during the August trapping periods attributable to heat exposure. Other causes of mortality were predation in traps (6), anesthesia overdose (2), and trap injury (2).

Fifteen non-target species were trapped, accounting for 2,467 captures (Appendix 1). Golden-mantled ground squirrels (*Spermophilus lateralis*), rock squirrels (*S. variegatus*), and Steller's jays (*Cyanocitta stelleri*) accounted for 89.0% of the captures. Significant seasonal differences in numbers of captures were evident (ANCOVA; $F = 23.6$; $df = 5,41$; $P < 0.001$). A total of 2,234 (90.6%) captures occurred during August 1996 and 1997; captures during both August periods were significantly greater than all other periods ($P < 0.001$-0.014). Other periods did not differ. The number of traps tripped by chipmunks and non-target species captures contributed to reduced tassel-eared squirrel capture success and lengthened the time necessary to obtain reliable population estimates.

Population Variable Estimates

Population and Density. We captured 450 squirrels (Table 1); 207 males (46.0%) and 243 females (54.0%). Capture probabilities were below minimum guidelines (0.3) to achieve reliable estimates (White et al. 1982) on 5 of 45 occasions. Population estimate standard errors averaged 10.2% (±1.0) for 45 estimates (Table 2). Standard errors >±10% occurred for 15 of 45 population estimates (Table 2), with most still

Table 1. Summary of 6 tassel-eared squirrel capture-recapture trapping efforts conducted 1996-97 at 8 study sites in north-central Arizona, including number of trap days, mean days trapped/period, total squirrel captures, individual squirrels by sex, trap days per capture, and trapping mortality.

	Capture-recapture trapping period						
Trapping parameter	Jan 1996	Apr 1996	Aug 1996	Jan 1997	Apr 1997	Aug 1997	All periods combined[1]
Trap days	12,672	10,368	9,648	5,184	7,776	10,368	56,016
Mean days trapped	11.0	9.0	8.4	5.1	7.7	9.0	8.5
Total squirrel captures	210	428	587	234	546	537	2,542
Individual squirrels:							
Male	48	81	106	64	97	81	207[1]
Female	52	78	126	62	78	96	243[1]
Total	100	159	232	126	175	177	450[1]
Trap days per:							
Capture	60.3	24.2	16.4	22.2	14.2	19.3	22.0
New squirrel	126.7	65.2	41.6	41.1	44.4	58.6	124.5[1]
Trapping mortalities (% of captures)	2 (0.9)	4 (0.9)	13 (2.2)	1 (0.4)	6 (1.1)	6 (1.1)	32 (1.3)

[1]Figures for individual squirrels and trap days per new squirrel reflect overlap in the number of individual squirrels that were caught during 1 or more periods.

Table 2. Tassel-eared squirrel captures and number of individual squirrels, population estimates ±standard error, 95% confidence intervals (CI), and population estimator (White et al. 1982) selected by program CAPTURE. Data are for 6 capture-recapture trapping efforts conducted 1996-97 at 8 study sites in north-central Arizona.

	Capture-recapture trapping period					
Study site (grid size)	Jan 96	Apr 96	Aug 96	Jan 97	Apr 97	Aug 97
Clints Well (71.8 ha)						
No. captures (squirrels)	21 (13)	23 (16)	37 (21)	18 (12)	60 (21)	20 (7)
Population estimate ±SE	16 ±2.88	18 ±3.77	21 ±1.50	16 ±3.94	23 ±2.56	--
95% CI	14-27	15-32	20-30	13-31	23-34	--
Estimator model[1]	M (h)	M (h)	M (bh)	M (h)	M (th)	--
Ft. Tuthill (61.9 ha)						
No. captures (squirrels)	4 (3)	39 (17)	117 (44)	33 (18)	76 (26)	191 (58)
Population estimate ±SE	5 ±1.97	20 ±2.98	45 ±1.47	19 ±1.44	28 ±1.87	64 ±3.73
95% CI	4-13	18-32	45-51	19-25	27-35	60-74
Estimator model[1]	M (h)	M (tb)	M (bh)	M (t)	M (th)	M (th)
Gash Flat (54.9 ha)						
No. captures (squirrels)	7 (3)	19 (8)	39 (14)	--	--	17 (5)
Population estimate ±SE	3 ±0.54	9 ±1.31	14 ±0.90	--	--	5 ±0.14
95% CI	3-3	8-15	14-20	--	--	5-5
Estimator model[1]	M (h)	M (h)	M (h)	--	--	M (bh)
Long Valley (70.7 ha)						
No. captures (squirrels)	44 (15)	37 (14)	33 (14)	16 (8)	65 (14)	19 (6)
Population estimate ±SE	15 ±1.49	14 ±0.85	12 ±0.5	8 ±1.03	14 ±1.33	6 ±0.24
95% CI	15-21	14-18	12-12	8-15	14-23	6-6
Estimator model[1]	M (h)	M (h)	M (bh)	M (h)	M (bh)	M (bh)
Marshall Mesa (71.6 ha)						
No. captures (squirrels)	52 (22)	75 (32)	95 (38)	76 (38)	94 (38)	78 (34)
Population estimate ±SE	22 ±1.42	33 ±2.44	41 ±2.87	41 ±2.12	39 ±1.61	36 ±1.50
95% CI	21-28	32-43	39-52	39-48	39-47	35-41
Estimator model[1]	M (th)	M (h)	M (bh)	M (t)	M (bh)	M (t)
Mormon Lake (71.0 ha)						
No. captures (squirrels)	23 (15)	41 (11)	43 (16)	12 (7)	35 (14)	41 (13)
Population estimate ±SE	15 ±2.31	11 ±1.71	17 ±0.89	8 ±1.59	14 ±0.91	15 ±2.11
95% CI	15-24	11-18	17-23	8-16	14-19	14-24
Estimator model[1]	M (h)	M (h)	M (th)	M (h)	M (th)	M (h)
Parks (59.9 ha)						
No. captures (squirrels)	11 (6)	60 (10)	92 (29)	21 (11)	75 (23)	37 (15)
Population estimate ±SE	6 ±1.17	19 ±1.82	31 ±2.20	12 ±1.52	24 ±1.54	15 ±1.01
95% CI	6-13	19-28	30-40	12-19	24-31	15-21
Estimator model[1]	M (h)	M (bh)	M (th)	M (h)	M (th)	M (t)
Pumphouse (63.4 ha)						
No. captures (squirrels)	48 (23)	149 (43)	131 (56)	58 (33)	141 (39)	134 (39)
Population estimate ±SE	26 ±2.49	43 ±0.94	57 ±3.26	43 ±4.81	39 ±0.88	43 ±2.82
95% CI	24-35	43-48	56-67	37-57	39-43	40-52
Estimator model[1]	M (h)	M (h)	M (th)	M (h)	M (tb)	M (th)

[1]Population estimator model sources of variation in squirrel capture probabilities (White et al. 1982):
M (t) - time
M (h) - heterogeneity
M (th) - time + heterogeneity
M (tb) - time + behavior
M (bh) - behavior + heterogeneity

Table 3. Tassel-eared squirrel survival rates (±standard error) for 4 periods in 1996-97, at 8 study sites in north-central Arizona. Estimates derived from program JOLLY. Letters denote differences among periods within each study site based on non-overlapping survival rate estimate 95% confidence intervals.

	Squirrel survival rate (±SE)				
Study site (*n*)	Apr 1996 - Aug 1996	Aug 1996 - Jan 1997	Jan 1997 - Apr 1997	Apr 1997 - Aug 1997	Mean
Clints Well (48)	0.75 ±0.12 A	0.66 ±0.15 A	0.66 ±0.12 A	--[1]	0.69 ±0.07
Ft. Tuthill (68)	--[2]	0.82 ±0.09 A	0.71 ±0.08 A	0.89 ±0.08 A	0.81 ±0.04
Long Valley (30)	0.86 ±0.16 A	0.63 ±0.16 A, B	0.54 ±0.15 B	--[2]	0.68 ±0.04
Marshall Mesa (78)	0.96 ±0.05 A	0.81 ±0.08 A, B	0.69 ±0.07 B	0.97 ±0.06 A	0.86 ±0.03
Mormon Lake (42)	0.71 ±0.17 A, B	0.88 ±0.10 A	0.42 ±0.14 B	0.93 ±0.17 A	0.73 ±0.05
Parks (53)	--[2]	0.92 ±0.08 A	0.69 ±0.12 A	0.74 ±0.17 A	0.85 ±0.04
Pumphouse (94)	0.77 ±0.08 A	0.97 ±0.05 B	0.70 ±0.07 A	0.84 ±0.06 A	0.82 ±0.03
Mean (n = 445)	0.81 ±0.12	0.81 ±0.10	0.63 ±0.10	0.91 ±0.11	0.78 ±0.04

[1] Trapping suspended - no estimate available.
[2] Insufficient sample size for previous period to compute survival rate.

<±15% ($\bar{x}$ = 17.7% ±1.7). Our Clints Well study site had 3 of 5 estimates with standard error >±15%, largely because of bait competition from other species; 1 other trapping effort was suspended as a result of low capture success associated with bait competition.

Population estimates varied widely among study sites from 3-64 squirrels per site, and among seasons within study sites (Table 2). Population estimates were lowest in January and highest in August (Table 2). In most instances significant differences existed among both seasonal populations and study sites based on non-overlapping 95% confidence intervals (Table 2). Five of the 6 available models in program CAPTURE (White et al. 1982, Pollock et al. 1990) were selected as the best population estimators accounting for behavioral, heterogeneity, and temporal influences on squirrel capture probabilities (Table 2).

Study site trap grid sizes ranged from 54.9 to 71.8 ha (Table 2) and were the base to compute uncorrected densities from population estimates. Mean uncorrected squirrel density did not differ among January (0.25/ha ±0.05, n = 15), April (0.35/ha ±0.04, n = 15), or August (0.44/ha ±0.08, n = 15) periods. Mean uncorrected squirrel density also did not differ between 1996 (0.33/ha ±0.04, n = 24) and 1997 (0.37/ha ±0.05, n = 21). For half the study sites, significant seasonal changes in uncorrected density were noted between January and August of each year: Ft.

Tuthill - 897%, Parks - 517%, and Gash Flat - 436% (Fig. 5). Other areas such as Marshall Mesa and Clints Well exhibited relatively stable uncorrected densities (Fig. 5).

Seasonal edge effect-corrected densities derived from program CAPTURE were generally more stable than uncorrected densities (Fig. 5). Mean corrected squirrel densities did not differ among the January (0.14/ha ±0.03, $n = 15$) or April and August periods, which were the same (0.17/ha ±0.03, $n = 15$). Mean corrected squirrel density did not differ significantly between 1996 (0.15/ha ±0.02, $n = 24$) and 1997 (0.18/ha ±0.03, $n = 21$). Only Ft. Tuthill failed to meet the program CAPTURE assumption of uniform density for computation of corrected densities (White et al. 1982) during both August periods.

During the March 1997 trapping in the area adjacent to Ft. Tuthill (300 trap days), proportionally more marked than unmarked squirrels were captured within 175 m of the study site edge than beyond that distance ($\chi^2 = 15.9$, $df = 1$, $P < 0.003$). We captured 17 previously marked squirrels in a narrow 13.5 ha band within 175 m of the study site edge. Only 1 unmarked squirrel was caught in this area. Beyond 175 m and outward to 385 m (16.2 ha), however, 7 unmarked squirrels were caught, while only 1 was marked.

Survival Rates. Squirrel survival rates averaged 0.78 (±0.03, $n = 24$) across all periods and 7 of 8 study sites (Table 3); estimates for Gash Flat were not attained as a result of inaccessibility during January and April 1997. For the 4 periods for which rates were calculated (Table 3), average survival ranged from 0.63 from January to April 1997, to 0.91 from April to August 1997. Significant differences were detected among periods (ANCOVA; $F = 10.1$; $df = 3,19$; $P < 0.001$). Mean winter survival (January to April 1997) was significantly lower ($P = 0.001$-0.024) than the other 3 periods, and the other 3 periods did not differ. In the period encompassing the squirrel hunting season (August 1996 to January 1997), survival rates averaged 0.81. Mean survival rates among study sites ranged from 0.68 to 0.86. Winter survival rates varied greatest among sites, from 0.42 to 0.71 (Table 3).

Recruitment. Trapping during 1996 and 1997 at Marshall Mesa and Ft. Tuthill (as part of a radio-telemetry study) yielded the best data for separating juvenile from adult squirrels. The November 1996 trapping yielded a distinct cohort of unmarked squirrels with mean weight of 523.0 g (±10.8, $n = 8$), 121.0 g less than the August 1996 mean for all captured squirrels (Appendix 2). Similar results were attained in November 1997, with mean juvenile weight of 539.0 g (±12.1, $n = 16$), 151.0 g less than the August mean for all squirrels (Appendix 2). The weight for 4 of 8 juveniles captured in November 1996 increased only 10-15 g upon recapture in January 1997. We therefore assumed that squirrels with weight ≤550 g in January were juveniles, compared to the mean for adults of 696.9 g (±17.5, $n = 69$). It was unlikely that squirrels ≤550 g were adults that had lost weight between August and January, as mean weight loss was only 17 g for recaptured adults (Appendix 2).

Eight juveniles (8.0% of total squirrels) were caught in January 1996, and 11 (8.7%) were captured in 1997. Most juveniles were captured at the Marshall Mesa study site: 37.5% of the total in 1996 and 45.4% in 1997. Using the January trapping period to estimate recruitment, juveniles/female averaged 0.15 (±0.05, $n = 7$) in 1996 and 0.13 (±0.05, $n = 7$) in 1997, which were not significantly different. Mean study site recruitment for both years ranged from 0.02 to 0.33 juveniles/female (Table 4).

Fitness. We estimated fitness for 7 of our 8 study sites; recruitment and survival data were lacking for Gash Flat. Fitness estimates varied from 0.003 to 0.094, and averaged 0.024 (±0.012) (Table 5).

Table 4. Tassel-eared squirrel recruitment rates (juveniles/female) measured in January 1996-97, at 8 study sites in north-central Arizona.

	Recruitment (juveniles/female)		
Study site	Jan 1996	Jan 1997	Mean
Clints Well	0.14	0.14	0.14
Ft. Tuthill	0.00	0.04	0.02
Long Valley	0.00	0.10	0.05
Marshall Mesa	0.23	0.42	0.33
Mormon Lake	0.28	0.00	0.14
Parks	0.33	0.16	0.24
Pumphouse	0.08	0.06	0.07
Mean	0.15	0.13	0.13

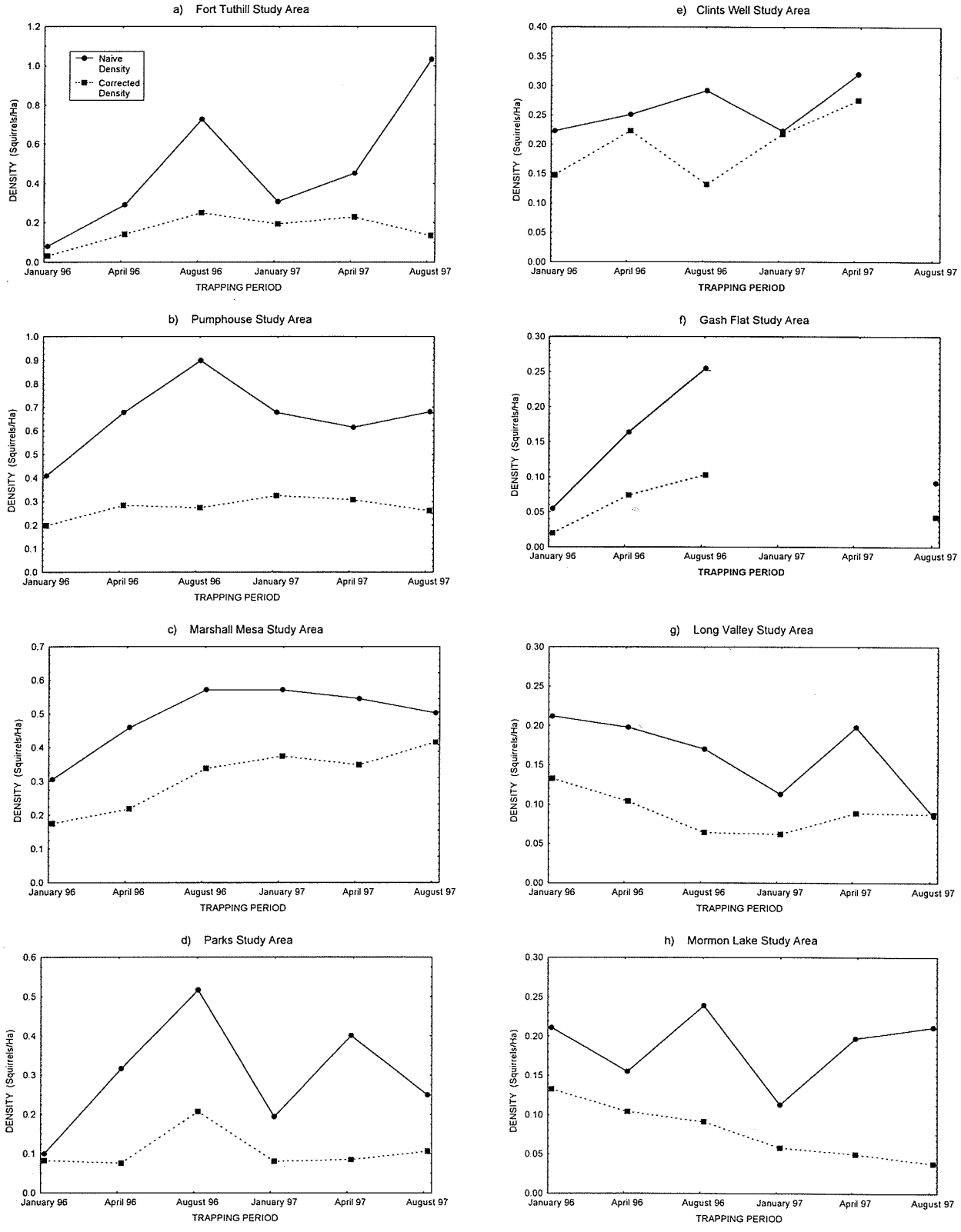


Figure 5. Seasonal tassel-eared squirrel uncorrected (= naive) and edge effect-corrected densities for 8 north-central Arizona study sites, 1996-97.

Table 5. Derivation of tassel-eared squirrel fitness values for 7 study sites in north-central Arizona, 1996-97.

Study site	$\bar{x}$ Corrected density/ha	X	$\bar{x}$ Recruitment (juveniles/female)	X	$\bar{x}$ Survival	=	Fitness
Clints Well	0.20	x	0.14	x	0.69	=	0.020
Ft. Tuthill	0.16	x	0.02	x	0.81	=	0.003
Long Valley	0.07	x	0.05	x	0.73	=	0.003
Marshall Mesa	0.33	x	0.33	x	0.86	=	0.094
Mormon Lake	0.08	x	0.14	x	0.73	=	0.008
Parks	0.11	x	0.24	x	0.85	=	0.022
Pumphouse	0.27	x	0.07	x	0.82	=	0.015
Mean	0.16	x	0.13	x	0.78	=	0.024

DISCUSSION

Our study was the first to use statistical rigor in estimating tassel-eared squirrel densities. Flyger (1959), Barkalow et al. (1970), Bouffard and Hein (1978), and Nixon et al. (1967) reported that the Schnabel population estimation method (Schnabel 1938) underestimated gray squirrel populations, as trap prone squirrels biased estimates. During our study, the rate of trap effort per capture dropped from 60.3 to 14.2 trap days/capture, reflecting an apparent trap prone response by squirrels. Program CAPTURE's various estimation models helped address the influence of squirrel behavioral and temporal response (White et al. 1982, Pollock et al. 1990).

Unlike most other studies of tassel-eared squirrels, we derived seasonal population and density estimates. Most studies of tassel-eared squirrels reported dramatic fluctuations in populations between years or habitat condition (Trowbridge and Lawson 1942, Keith 1965, Stephenson and Brown 1980, Hall 1981, and Patton et al. 1985). Like Farentinos (1972*a*), we found similar average densities during the 2 years of our project and dramatic seasonal fluctuations within each year of our study. Farentinos (1972*a*) attributed a 67% increase in density from spring to fall to recruitment of juveniles, as did Keith (1965), and a 55% decline the following spring to mortality and emigration.

Unlike Farentinos (1972*a*) and Keith (1965), the dramatic increases in uncorrected squirrel density on several study sites from April to August (Fig. 5) was probably not a function of juvenile recruitment, which averaged only 0.17 juveniles/female in 1996 and 1997. This low recruitment was well below the level considered unusually low (0.50 juveniles/female) by Brown (1984). Low recruitment observed in our study probably reflected a combination of habitat condition, food availability, weather, and predation. Drought conditions experienced prior to and during our study may have affected food availability, especially hypogeous fungi and consequently squirrel recruitment. Only 2 study sites exhibited increases in corrected density throughout the duration of our study; Marshall Mesa (+138%) and Clints Well (+86%). These sites had the highest and third highest recruitment rates, respectively. The nominal recruitment at Marshall Mesa, coupled with high average survival was sufficient to allow for an increasing population even under drought conditions (Fig. 5). Conversely, Mormon Lake, with poor recruitment, relatively low average survival, and the lowest winter survival, displayed a steadily declining population (-71%; Fig. 5). Differential sport hunting impact on juveniles among study sites prior to January may have been a source of potential bias in our recruitment estimates. Also, our estimates accounted only for those juveniles alive and present on study sites in January.

Since fluctuations in uncorrected density

were apparently not attributable to low recruitment, we postulated that they were food-availability related and attributable to: 1) expanded home ranges of squirrels primarily residing adjacent to study sites, and/or 2) squirrels that emigrated to study sites from population "source" areas. Observed peak uncorrected densities that occurred during late summer coincided with peak food availability reported at other areas in late summer-fall by Stephenson (1975), Hall (1981), Brown (1984), and States et al. (1988), particularly pine cone seed and hypogeous fungi. These 2 foods are important in determining squirrel distribution, abundance, and survival (States and Wettstein 1998). Keith (1965), Hall (1981), and Patton et al. (1985) demonstrated the importance that cone seeds played in localized population fluctuations.

Several of our study sites were heavily logged in the past reducing canopy closure and basal area, and possibly hypogeous fungi production, an effect reported in other studies (Pederson et al. 1987, States and Gaud 1997). Evidence of fungi use by squirrels (digs) during our study was low compared to other studies where fungi were prevalent in squirrel diets (Stephenson 1975, States et al. 1988). Fungi production may have been limited by drought conditions. With apparent low availability of fungi fruiting bodies, reliance on pine cones for seeds may have been heightened at some sites.

Study sites that otherwise appeared to be structurally marginal habitat because of low basal area, canopy closure, and interlocking canopy trees (Pederson et al. 1976, 1987; Patton 1984, Patton et al. 1985) supported high squirrel densities during periods of high cone availability. Cone production at these sites may have been enhanced as a result of the thinned, non-competing nature of remaining trees (Schubert 1974, Buchanan et al. 1990).

Home ranges of squirrels primarily residing adjacent to study sites may have expanded onto study sites in increased numbers when cones were available (August) and then shrunk once cones were depleted (January), thus providing a possible explanation for density fluctuations. Home ranges of squirrels on or immediately adjacent to heavily logged study sites may have been larger than those of squirrels on unlogged or selectively logged sites. Pederson et al. (1976) and Patton et al. (1985) documented 83% to 356% increases in squirrel home-range sizes following logging. We noted a consistent pattern of some squirrels appearing on study sites only during the period when cones were abundant. For instance, 12 squirrels caught initially at 4 study sites in August 1996 were not caught again until August 1997. Conversely, on the same sites, only 3 squirrels were caught during 2 or more January and April trapping periods, but not during either August period. Peak August squirrel densities may have been influenced by the attractive nature of our bait. However, such an attraction was also present during the January and April periods when food was more limiting, yet lower densities were attained. As such, we believe our baiting posed no major bias in our density estimates.

Many authors have stressed the role of immigration and emigration in small mammal population dynamics (Lidicker 1975, Van Horne 1983, Wauters and Dhondt 1993). Wauters and Dhondt (1993) reported on immigration patterns of European red squirrels (*Sciurus vulgaris*) and identified 2 main immigration periods; spring and late summer-fall. Spring immigration coincided with the breeding season, while late summer-fall immigration coincided with seed crop availability. On our study sites, uncorrected density increased at most areas between January and April, at the onset of breeding. We noted more dramatic increases in density during August, which just preceded pine cone maturation and highest seed nutrient value (States et al. 1988).

Consistent with Wauters and Dhondt (1993), we observed an increased proportion of males during the spring breeding period (53% versus 46% for the entire study) and a preponderance of females during the summer-fall period (54%). Males residing adjacent to study sites possibly widened their activity areas onto our sites to increase mating opportunities. Males and females alike moved onto some study sites in late summer-fall when cone crops were available. Natal dispersal by juveniles in fall, reported by Wauters and Dhondt (1993), was not observed, probably since recruitment was low. However, subadult or yearling squirrels (10-14 months old) may have contributed to observed density increases in April and August, a pattern observed for gray squirrels (Teaford 1986).

Van Horne (1983) hypothesized that high animal densities in lower-quality habitat may be a function of juvenile, subadult, or yearling immigration into "sinks" where social interactions are limited. Without strong social, density-limiting interactions, dispersing animals from source areas may build to high densities in sinks. At some of our study sites of apparent lower quality habitat, high August uncorrected densities were comprised primarily of non-resident squirrels that were absent at other times. Such

areas also exhibited low recruitment. Our results were consistent with Van Horne (1983), who described higher-quality habitats as those where densities are lower but stable and reproduction is more dependable even under poor conditions.

Only 2 of our 8 study sites appeared to function as dispersal source areas (Marshall Mesa and Clints Well); other sites exhibited patterns typical of dispersal sinks with limited recruitment. Source area squirrel densities did not fluctuate as others did and populations increased even under severe drought conditions. Even under these conditions, source areas with high quality habitat similar to Marshall Mesa probably produced surplus squirrels that ultimately dispersed to adjacent lower quality habitats.

We presumed that squirrels left dispersal sink study sites by January, when densities were lowest, as a result of depletion of cone crops and movement to habitat of higher quality necessary for winter survival. Radio-telemetry monitoring at our Ft. Tuthill site confirmed that most squirrels departed the site during winter and resided in adjacent unlogged habitat (Lema et al. *In press*). Trapping conducted adjacent to Ft. Tuthill in March 1997 also confirmed that most squirrels left the area to reside along a relatively narrow, adjacent band of quality habitat. Squirrels in this area appear to have adapted socially to high seasonal densities (>1 squirrel/ha) at a time when winter food (e.g., pine twig inner cambium) was abundant. Lema et al. (*In press*) found that 53% of radio-collared squirrels (n = 28) shared nests with other squirrels during winter, possibly conferring benefit to survival through thermoregulation. Winter squirrel survival was higher at Ft. Tuthill than our other sites, suggesting a benefit from adjacent cone crops, seasonal shifts in habitat use, and social interactions. Population dynamics at Ft. Tuthill and other sites adjacent to areas apparently functioning as dispersal source areas have landscape-scale management implications.

CHAPTER II

DEVELOPMENT AND EVALUATION OF TASSEL-EARED SQUIRREL POPULATION INDEX TECHNIQUES

METHODS

Index Counts

We made index counts at each study site in conjunction with squirrel trapping sessions, with the exception of nest counts which were conducted only once. Except where noted, all index counts were made by the same observer to maintain consistency.

Track Counts. We counted tassel-eared squirrel track sets on snow during the second winter under excellent conditions; >30 cm depth and several days of settling to allow surface traversing by squirrels. Counts were conducted simultaneously in January 1997 by 16 observers on study sites under similar snow conditions. We counted track sets crossing or within sight of lines connecting the interior 100 trapping points (7.0 km of line transect per site) (Fig. 4). We analyzed both total track sets and number of 70 m intervals (maximum $n = 100$) between trapping points with squirrel track sets. The latter measure was used to reduce bias associated with counting multiple sets of tracks from the same squirrel.

In addition to snow track counts, we tallied "hits" at baited track stations (Fig. 6) constructed of plastic rain gutter with aluminum track plates inside (Drennan et al. 1998). Track plates were sprayed with carpenter's chalk and alcohol; when the alcohol evaporated a track bed was left. Track stations were baited with peanut butter and oatmeal. We did track counts immediately prior to or after all trapping periods except January 1996. Track stations were placed at the 100 inner trapping points (Fig. 4) and were left for 2 days.

Track "hits" were identified and recorded (Drennan et al. 1998). We evaluated the seasonal impact of non-target species bias on track counts by assessing the number of track plates rendered unreadable.

Feeding Sign Counts. We counted feeding sign on 2 different sized plots: 1) 20-m^2 plots centered on the inner 100 trapping points, and 2) 400 1-m^2 plots spaced approximately 17.5 m apart along the 10 trapping lines (Fig. 4). Counts were typically completed within 1 month following trapping. Types of sign counted were: 1) ponderosa pine clipped terminal needle clusters (clippings), 2) twigs from which the bark had been peeled away and the inner cambium layer consumed by squirrels (peeled twigs), 3) discarded ovulate cone cores from which squirrels consumed seeds, and 4) hypogeous fungi (and cone) digs (Rasmussen et al. 1975, Brown 1984). Since plots were not cleared of sign prior to counts, only fresh sign was counted (Rasmussen et al. 1975, Brown 1984). Fresh sign included green clippings, white peeled twigs, bright orange or red cone cores, and digs not covered by litter or partially filled in with soil.

Nest Counts. We counted squirrel nests from the same 7.0 km lines described above for snow track counts (Fig. 4), during fall 1997. We classified nests as active (greenish nest material present) or inactive (brown or in a state of disrepair). We measured perpendicular distances from the transects to observed nests. We used the program DISTANCE (Burnham et al. 1980, Buckland et al. 1993, Laake et al. 1996) to estimate nest densities for study sites. Two independent sets of nest counts were done at each study site to assess observer bias. One observer counted nests at all 8 study sites while 4 other observers counted nests at 2 study sites each.

Track Count Power Analysis

We used bootstrap simulations (Efron and Gong 1983) to assess performance of multiple, alternative track station index designs. Our objective was to identify designs and minimum number of track stations required to maintain high correlation with squirrel density. We evaluated 2 reduced-effort designs: 1) square track station grids ranging in size from 4 X 4 to 9 X 9, and 2) sets of 2-9 randomly-selected lines with 10 track stations per line. Only April 1996 and 1997 track count data were used in the simulations based on the strength and consistency of the correlations between track counts and uncorrected squirrel density. Simulations were programmed using QuattroPro® v8 macro language.

We conducted 2 simulation analyses for each reduced-effort sampling design. The first simulation derived the expected distribution of track counts under each design, using a bootstrap sample of 1,000 sites from the original data set. After each site was drawn, the sampling array (grid or random lines) was superimposed on the original track station data matrix, then the total number of track "hits" was counted and stored. Grids were randomly located within the boundaries of the full 10 X 10 grid array. Random line arrays were simulated by randomly selecting an appropriate number of rows or columns from the full 10 X 10 array. Line orientation (row- or column-wise) was randomized each time a site was drawn. We

calculated the 25th, 50th, and 75th percentiles of each bootstrap sample, representing "low," "medium," and "high" counts expected under that sampling design.

The second simulation evaluated the predictive power of each reduced-effort design. This procedure consisted of 3 steps; step 1 drew a bootstrap sample of 15 sites from the original data set. After a site was drawn, the sampling array was applied as was done in the first simulation. The total number of track "hits" was counted and paired with the corresponding baseline squirrel uncorrected density estimate (from program CAPTURE) for that trapping event. Step 2 fit a simple linear regression model to the bootstrap sample, using squirrel density as the dependent variable and total track hits as the independent variable. Parameter estimates from the regression were used to calculate 90% and 95% prediction intervals (Zar 1984) around "low," "medium," and "high" counts expected under that sampling design. Steps 1 and 2 were repeated 1,000 times, storing regression results and prediction intervals from each iteration. The third and final step was calculation of summary statistics from all 1,000 iterations. We used the mean coefficient of determination (r^2) as a measure of the overall relationship between track counts and squirrel density estimates for each sampling design. The frequency of overlap between prediction intervals was used to estimate the power of each design to detect differences in squirrel density. For example, if the "low" and "medium" prediction interval overlapped in 50 of 1,000 iterations, estimated powe was 1,000-50/1,000 = 95%. We also calculated mean regression intercept and beta coefficient value for each design.

Index Technique Evaluation

During April and May 1998, we evaluated 3 index techniques at the 3 Camp Navajo and 3 of 6 Mount Trumbull sites: 1) a reduced-effort track station design, 2) a similarly reduced-effort feeding sign index incorporating all types of sign, and 3) a combined technique using track count and all feeding sign. Track station counts only were made at the other 3 Mount Trumbull sites. We evaluated and compared squirrel index estimates and prediction intervals, labor costs, and observer bias for each technique. Track station and feeding sign index counts were made using the optimum reduced-effort design derived from the power analysis for track station data, though a similar analysis has not been completed for feeding sign data. Track station track plates and 1-m^2 feeding sign plots were read by 2 sets of 4 observers at each validation area to evaluate bias associated with identifying tassel-eared squirrel tracks and feeding sign.

We evaluated and compared all index techniques across sampling periods for potential application in estimating tassel-eared squirrel densities. The criterion by which population

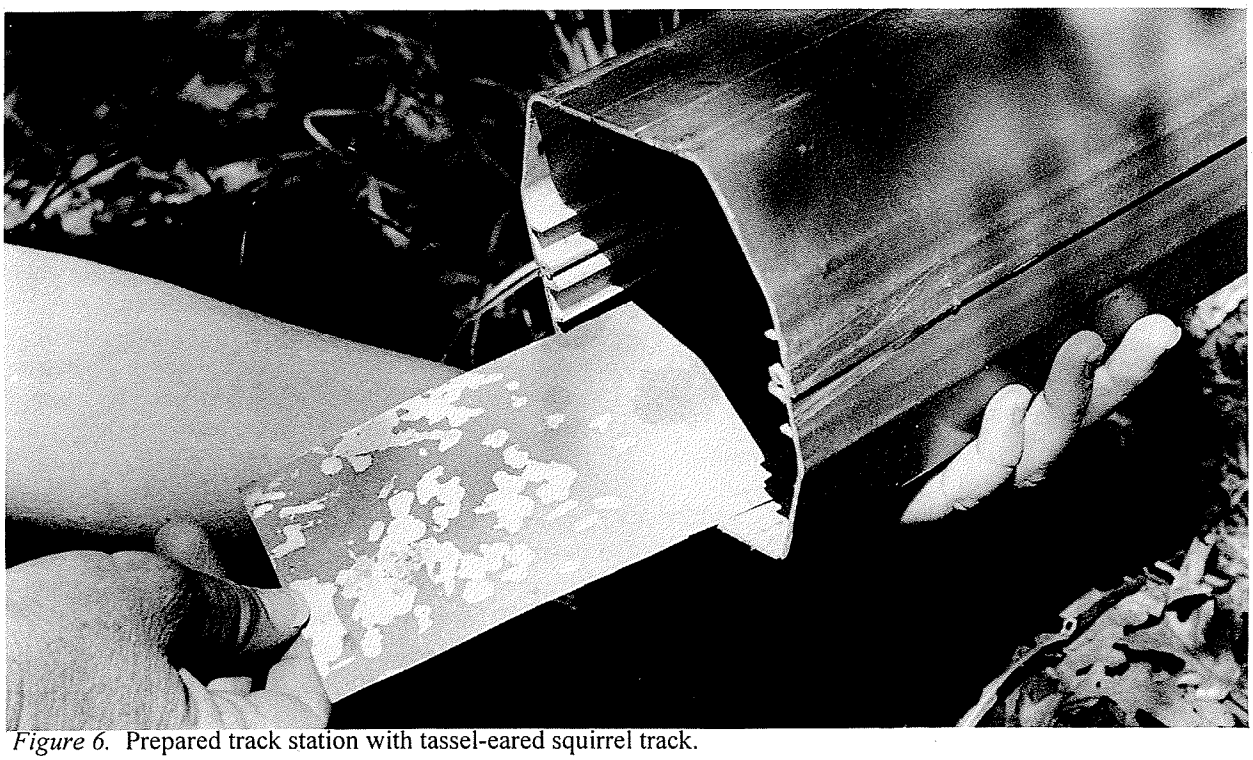


Figure 6. Prepared track station with tassel-eared squirrel track.

index techniques were evaluated was the degree to which they were: 1) reliable, with high accuracy and precision in estimating true squirrel density, and low type I and II error rates; 2) consistent in application and results (i.e., same relationships between years and among observers); and 3) efficient in application relative to time and cost.

Statistical Analyses

All statistical tests were performed using the program STATISTICA® (Statsoft, Inc. 1994). Results of all statistical tests were considered significant at $P \leq 0.05$. Mean values are reported with ± standard errors.

Index Counts. We assessed feeding sign differences between sampling periods for mean frequency of occurrence (1-m^2 plots) and abundance (1-m^2 and 20-m^2 plots) using analysis of covariance (ANCOVA). We assessed differences in feeding sign by removing the influence of study site effects from the comparison among periods (Hays 1981). For significant ANCOVAs, we assessed pairwise differences between periods with Sheffe's multiple comparison tests. We applied $\sin^{-1}$ transformations to all feeding sign frequency of occurrence data, and square root transformations to all abundance data prior to ANCOVA (Steel and Torrie 1980).

We evaluated differences in track station and feeding sign (1-m^2 plot frequency) index counts by study site using multiple pairwise comparisons (Drennan et al. 1998). Differences were assessed relative to the null hypothesis that both samples being compared were drawn from a binomial distribution with the expected value equal to the mean of the 2 observations with $n = 100$ (track stations) or $n = 400$ (feeding sign plots). Pairwise comparisons were then made between index counts (track station and feeding sign) and baseline population estimates by study site and sampling period to assess type I and II error rates. For instance, if a comparison between 2 study sites indicated that their populations were not different (based on overlapping 95% confidence intervals), but the track station counts differed, we assumed a type I error for the index value. Conversely, if 2 squirrel populations differed significantly, but the track station counts were not different, we concluded a type II error had occurred in the index method.

We employed ANCOVA and Scheffe's multiple comparison tests to assess differences in unreadable track stations among periods attributable to non-target species, removing the influence of study sites. We used simple linear regression to measure the relationship between number of non-target species captures and number of unreadable track stations ($\sin^{-1}$ transformed) associated with each trapping period.

As part of our evaluation of 3 index techniques used at Camp Navajo and Mount Trumbull, we used ANCOVA and Sheffe's test to assess differences in squirrel density estimates derived by track station, combined feeding sign, and the combined track station and feeding sign index techniques. ANCOVA adjusted for the influence of evaluation site effects. We used the same tests to assess differences in the width of squirrel density prediction intervals among techniques.

Index Count Observer Bias and Concordance. We employed nonparametric Friedman analysis of variance (ANOVA) to assess differences in 3 data sets: the number of active and inactive nests counted among observers at the 8 primary study sites, and track station and combined feeding sign counts among each group of observers at Camp Navajo and Mount Trumbull. Nest count sampling units used in the comparisons were the trapping lines with 10-70 m intervals per line (n = 10 per study site, total $n = 80$). Nest count comparisons were made between the single observer counts for all 8 study sites and the corresponding counts for 2 study sites each by the other 4 observers. We used Kendall concordance coefficients (Hays 1981) to assess inter-observer reliability and consistency in counting nests, tracks, and feeding sign.

Regression Analysis. We evaluated the ability of each index count to predict squirrel density with simple and multiple regression analyses (Neter and Wasserman 1974). We used uncorrected densities in most analyses, as all squirrels present on study sites influenced index counts, regardless of edge effect. Corrected density was used for nest count analysis, since we assumed that only resident squirrels built nests. Separate analyses were conducted for individual sampling periods and each year, and years combined if they did not differ from each other. To assess regression assumptions, we examined normal probability plots of residuals and plotted predicted versus residual scores (Neter and Wasserman 1974). We applied $\sin^{-1}$ transformations to all variables expressed as decimal fractions or percentages (e.g., frequency of occurrence of feeding sign, track station counts) and square root transformations to count data (feeding sign abundance) prior to regression analysis (Steel and Torrie 1980).

We used analysis of covariance (ANCOVA) and subsequent multiple comparisons to assess differences in slopes of regression lines among seasons for squirrel density and index counts (Hays 1981, Statsoft, Inc. 1994). For regressions yielding strong relationships ($r^2 > 0.900$), both 95% and 90% prediction intervals (Zar 1984) were computed for application as a population index technique to predict squirrel density.

RESULTS

Index Counts

Track Counts. During January 1997, we counted an average of 30.4 (±7.3) sets of squirrel tracks at 7 study sites; some tracks probably were from the same squirrels. These track sets occurred on an average of 22.0 (±4.3) of 100 trapping station intervals. The relationship between the number of sets of tracks and uncorrected density ($n = 5$) for January 1997 was not significant ($r^2 = 0.223$, $P = 0.284$), as was the relationship with number of intervals with tracks ($r^2 = 0.261$, $P = 0.242$). While snow conditions were excellent during our simultaneous snow track counts, variable snow conditions could present a problem with this technique. Subsequent to placement of 500 track stations in January 1997, of which 232 (46.4%) had positive tassel-eared squirrel "hits," very few (<10) squirrel tracks were noted in the snow near visited track stations because of melting and crusting of the snow surface.

Strong and significant relationships existed between track station counts and uncorrected densities. Slopes of the regressions differed among the 5 periods assessed (ANCOVA; $F = 7.3$; $df = 4,25$; $P < 0.001$). Relationships between uncorrected densities and track counts were strongest in April (1996, $r^2 = 0.924$, $P < 0.001$, $n = 8$; 1997, $r^2 = 0.927$, $P < 0.001$, $n = 7$), and regression slopes did not differ (ANCOVA; $F = 0.16$; $df = 1,11$; $P = 0.701$) (Fig. 7). The August 1997 regression was the weakest ($r^2 = 0.736$, $P = 0.026$, $n = 7$) and its slope differed (ANCOVA; $F = 12.18$; $df = 1,11$; $P = 0.005$) from the August 1996 regression ($r^2 = 0.810$, $P = 0.002$, $n = 8$). The regression for August 1997 also differed from both April regressions (ANCOVA; 1996; $F = 31.78$; $df = 2,11$; P < 0.001; 1997; $F = 12.41$; $df = 2,10$; $P = 0.005$). The January regression was only marginally significant ($r^2 = 0.780$, $P = 0.047$, $n = 5$) and did not differ from the other 4 periods. Owing to consistency between years during April, the combined regression ($r^2 = 0.925$, $P < 0.001$, $n = 15$) (Fig. 7) yielded narrow 90% and 95% density prediction intervals (Fig. 8).

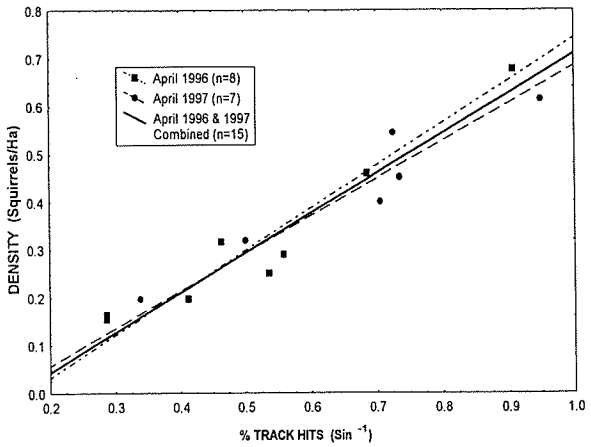


Figure 7. Regression of April tassel-eared squirrel uncorrected density/ha and number of track stations with squirrel hits (sin^{-1} transformed) at 8 north-central Arizona study sites. Lines represent April 1996-97 combined, and 1996 and 1997 individually. Combined $r^2 = 0.925$, $P < 0.001$, $n = 15$.

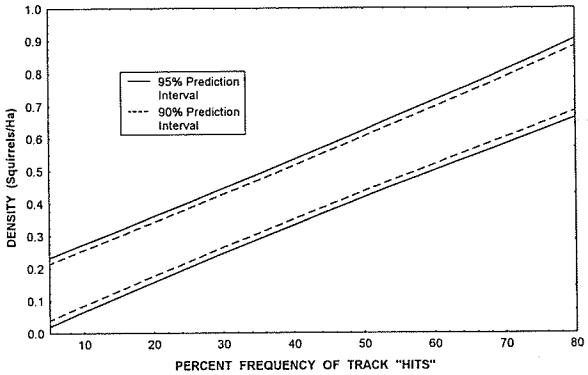


Figure 8. Prediction intervals (90% and 95%) around regression line for combined April 1996-97 tassel-eared squirrel uncorrected density/ha and percent frequency of track stations with squirrel hits derived from 8 north-central Arizona study sites.

In examining type I and type II error rates for comparisons of track counts and squirrel populations between study sites, we found that April and August were similar. The combined error rate for April 1996 and 1997 comparisons ($n = 49$) was 22.4% (type I-14.3%, type II-8.2%). For August combined ($n = 49$), 26.5% of comparisons resulted in errors (type I-10.2%, type II-16.3%).

Track station visits by non-target species varied from 7.6% of track stations in January 1997 to 71.0% in August 1996. August 1996 and 1997 visits averaged 68.1%, and April visits averaged 43.1%. The number of unreadable track stations also varied by period and ranged from 2.6% in April 1996 to 22.6% in August 1997, and differed significantly among periods (ANCOVA;

$F = 7.7$; $df = 5,29$; $P = 0.002$). The mean number of unreadable track stations in August 1997 was significantly greater than all others ($P = 0.001$-0.010) except August 1996; no other comparisons were significant. The number of track stations rendered unreadable was highly associated with the number of non-target species captures during each trapping period ($r^2 = 0.954$, $P = 0.004$, $n = 5$).

Feeding Sign Counts. We counted squirrel feeding sign on a total of 12,660 1-m^2 plots and 3,165 20-m^2 plots during 5 periods; as a result of deep snow, counts were not conducted following the January 1997 trapping effort. Seasonal fluctuations were evident for both feeding sign frequency of occurrence on 1-m^2 plots (Table 6) and abundance on 20-m^2 plots (Table 7).

Mean percent frequency of occurrence of fungi digs on 1-m^2 plots showed significant differences among seasons (ANCOVA; $F = 16.2$; $df = 4,31$; $P < 0.001$). January 1996 frequency of occurrence was significantly higher than other periods ($P < 0.001$), among which fungi occurrence did not differ (Table 6). The relationship between squirrel uncorrected density and fungi occurrence was significant for January 1996 ($r^2 = 0.652$, $P = 0.015$, $n = 8$) and April 1996 ($r^2 = 0.801$, $P = 0.001$, $n = 8$). Mean fungi dig abundance on 20-m^2 plots also differed among seasons (ANCOVA; $F = 9.2$; $df = 4,31$; $P <$ 0.001). January 1996 fungi dig abundance was significantly higher ($P = 0.001$-0.038) than other periods (Table 7). No relationships between fungi dig abundance and uncorrected density were significant.

Cone core frequency of occurrence on 1-m^2 plots, and abundance on 20-m^2 plots did not differ significantly among periods (Tables 6 and 7). Cone core occurrence on 1-m^2 plots was significantly related to uncorrected density during all periods except January 1996 (Table 6), and slopes of regression lines did not differ among periods (ANCOVA; $F = 0.9$; $df = 4,4$; $P = 0.436$). The pooled August 1996 and 1997 relationship between 1-m^2 plot cone core frequency of occurrence and uncorrected density was strong ($r^2 = 0.783$, $P = 0.001$, $n = 15$). Only August 1996 yielded a significant relationship between cone core abundance on 20-m^2 plots and uncorrected density (Table 7). Slopes of regression lines for 20-m^2 plot cone abundance and uncorrected density did not differ among periods (ANCOVA; $F = 0.5$; $df = 4,4$; $P = 0.743$).

The relationship between cone core frequency of occurrence on 1-m^2 plots and abundance on 20-m^2 plots was poor ($r^2 = 0.317$, $P = 0.317$, $n = 35$), while for other types of feeding sign the relationships were good ($r^2 > 0.800$). A disproportionately small number of plots exhibited high squirrel feeding activity indicative of preferred feed trees; 1.1% of 20-m^2 plots contained 19.2% of all cone cores.

The incidence of type I and II error rates in pairwise comparisons of cone core sign and population estimate comparisons between study sites was 23.8% for both August periods combined. Type II errors associated with cone feeding sign (19.0%) outnumbered type I errors (4.8%) nearly 4 fold, indicating a potential insensitivity of this technique to detect differences in squirrel density.

Seasonality in feeding sign was most apparent for terminal clippings and peeled twigs (Tables 6 and 7). These types of sign were most prevalent in late winter-spring when other foods were limited or unavailable. Because of the common origin of these 2 types of sign, there was a strong association between frequency of occurrence of peeled twigs and terminal clippings on 1-m^2 plots ($r^2 = 0.852$, $P < 0.001$, $n = 35$), and abundance on 20-m^2 plots ($r^2 = 0.939$, $P < 0.001$, $n = 35$). Differences among seasons for mean frequency of occurrence of clippings were evident (ANCOVA; $F = 38.8$; $df = 4,31$; $P <0.001$) (Table 6), as they were for abundance on 20-m^2 plots (ANCOVA; $F = 13.9$; $df = 4,31$; $P < 0.001$) (Table 7). Clipping occurrence ($P < 0.01$) and abundance ($P = 0.033$-0.043) during April 1996 and 1997 were significantly higher than other periods; the April periods did not differ.

Relationships between terminal clipping frequency of occurrence on 1-m^2 plots and squirrel uncorrected density were significant for all periods, except August 1996 (Table 6). Relationships involving 20-m^2 plot abundance were significant for all periods except August 1997 (Table 7). Regressions of clipping occurrence on 1-m^2 plots and uncorrected density differed among periods (ANCOVA; $F = 10.1$; $df = 4,4$; $P < 0.001$), as did regressions for abundance on 20-m^2 plots (ANCOVA; $F = 8.0$; $df = 4,4$; $P < 0.001$). For clipping occurrence and abundance, regressions for the April periods were similar and differed from the 2 August periods, but not January 1996.

Type II errors (24.4%) in pairwise comparisons of April terminal clipping counts and populations greatly outnumbered type I errors (2.1%), by a factor of 12 . The total error rate was 26.5%.

The frequency of occurrence of all types of sign combined on 1-m^2 plots differed among

Table 6. Tassel-eared squirrel feeding sign on 1-m² plots (400 plots/area/period) at 8 study sites in north-central Arizona 1996-97. Summary includes mean percent frequency of occurrence ±standard error, results of regression with uncorrected squirrel density/ha, and differences among seasons (different letters among periods indicate significant differences; ANCOVA and Sheffe's post hoc tests, $P \leq 0.05$).

	Sampling period				
Feeding sign type	Jan 1996	Apr 1996	Aug 1996	Apr 1997	Aug 1997
Fungi digs					
Mean % freq. of occurrence ±SE	19.50 ±3.88	6.85 ±1.98	3.00 ±0.73	4.99 ±1.72	2.47 ±1.33
Regression with uncorrected density:					
Correlation coefficient (*r*)	0.817	0.927	0.437	0.752	0.131
	$P = 0.013$	$P = 0.001$	$P = 0.326$	$P = 0.051$	$P = 0.779$
Coefficient of determination (r^2)	0.667	0.861	0.182	0.565	0.017
Differences among seasons	A	B	B	B	B
Cone cores					
Mean % freq. of occurrence ±SE	14.63 ±1.89	14.81 ±2.45	16.89 ±3.79	8.56 ±2.53	8.66 ±3.44
Regression with naive density:					
Correlation coefficient (*r*)	0.151	0.857	0.873	0.774	0.871
	$P = 0.722$	$P = 0.006$	$P = 0.010$	$P = 0.041$	$P = 0.011$
Coefficient of determination (r^2)	0.023	0.734	0.762	0.599	0.759
Differences among seasons	A	A	A	A	A
Peeled twigs					
Mean % freq. of occurrence ±SE	2.56 ±0.87	6.06 ±1.96	0.19 ±0.19	6.72 ±1.79	0.00 ±0.00
Regression with naive density:					
Correlation coefficient (*r*)	0.859	0.955	0.692	0.870	N/A
	$P = 0.007$	$P < 0.001$	$P = 0.085$	$P = 0.011$	
Coefficient of determination (r^2)	0.626	0.881	0.612	0.893	N/A
Differences among seasons	A, B	A	B	A	B
Terminal clippings					
Mean % freq. of occurrence ±SE	8.25 ±2.03	17.60 ±3.04	2.71 ±1.47	23.14 ±3.12	0.21 ±0.21
Regression with naive density:					
Correlation coefficient (*r*)	0.754	0.871	0.734	0.909	0.784
	$P = 0.031$	$P = 0.005$	$P = 0.060$	$P = 0.005$	$P = 0.037$
Coefficient of determination (r^2)	0.569	0.759	0.539	0.826	0.615
Differences among seasons	A	B	A	B	A
All sign					
Mean % freq. of occurrence ±SE	37.06 ±4.58	33.20 ±5.45	21.00 ±3.96	32.49 ±5.05	7.51 ±3.29
Regression with naive density:					
Correlation coefficient (*r*)	0.855	0.983	0.963	0.982	0.617
	$P = 0.007$	$P < 0.001$	$P < 0.001$	$P < 0.001$	$P = 0.139$
Coefficient of determination (r^2)	0.731	0.966	0.927	0.964	0.381
Differences among seasons	A	A	B	A	B

Table 7. Tassel-eared squirrel feeding sign on 20-m^2 plots (100 plots/area/period) at 8 study sites in north-central Arizona 1996-97. Summary includes mean number items per plot ±standard error, results of regression with uncorrected squirrel density/ha, and differences among seasons (different letters among periods indicate significant differences; ANCOVA and Sheffe's post hoc tests, $P \leq 0.05$).

	Sampling period				
Feeding sign type	Jan 1996	Apr 1996	Aug 1996	Apr 1997	Aug 1997
Fungi digs					
Mean no. plot ±SE	1.39 ±0.36	0.53 ±0.13	0.16 ±0.05	0.45 ±0.15	0.16 ±0.07
Regression with uncorrected density:					
Correlation coefficient (r)	0.256	0.792	0.078	0.541	0.122
	$P = 0.541$	$P = 0.190$	$P = 0.854$	$P = 0.292$	$P = 0.795$
Coefficient of determination (r^2)	0.065	0.627	0.066	0.293	0.015
Difference among seasons	A	B	C	B	C
Cone cores					
Mean no. plot ±SE	5.83 ±2.45	4.68 ±1.87	2.61 ±0.73	1.82 ±0.72	3.09 ±1.16
Regression with naive density:					
Correlation coefficient (r)	0.230	0.307	0.844	0.416	0.627
	$P = 0.584$	$P = 0.094$	$P = 0.008$	$P = 0.354$	$P = 0.132$
Coefficient of determination (r^2)	0.053	0.094	0.712	0.173	0.393
Difference among seasons	A	A	A	A	A
Peeled twigs					
Mean no. plot ±SE	0.39 ±0.20	1.54 ±0.59	0.02 ±0.01	1.51 ±0.52	0.00 ±0.00
Regression with naive density:					
Correlation coefficient (r)	0.866	0.844	0.698	0.808	N/A
	$P = 0.005$	$P = 0.008$	$P = 0.055$	$P = 0.028$	
Coefficient of determination (r^2)	0.750	0.712	0.487	0.653	N/A
Difference among seasons	A	A	A	A	A
Terminal clippings					
Mean no. plot ±SE	1.10 ±0.48	3.59 ±1.10	0.20 ±0.15	3.81 ±1.07	0.10 ±0.07
Regression with naive density:					
Correlation coefficient (r)	0.819	0.777	0.761	0.819	0.422
	$P = 0.013$	$P = 0.023$	$P = 0.028$	$P = 0.024$	$P = 0.178$
Coefficient of determination (r^2)	0.671	0.604	0.579	0.671	0.178
Difference among seasons	A	B	A	B	A
All sign					
Mean no. plot ±SE	8.72 ±2.63	10.34 ±2.87	3.00 ±0.83	7.60 ±1.77	3.34 ±1.25
Regression with naive density:					
Correlation coefficient (r)	0.035	0.708	0.891	0.853	0.612
	$P = 0.934$	$P = 0.050$	$P = 0.003$	$P = 0.016$	$P = 0.144$
Coefficient of determination (r^2)	0.001	0.501	0.794	0.728	0.374
Difference among seasons	A	A	A	A	A

seasons (ANCOVA; $F = 6.7$; $df = 4,31$; $P < 0.001$) (Table 6), as did abundance on 20-m^2 plots (ANCOVA; $F = 13.9$; $df = 4,31$; $P < 0.001$). Combined feeding sign occurrence for August 1997 was significantly lower than the other periods ($P = 0.002$-0.020), except August 1996 (Table 6). Both August periods had significantly lower combined feeding sign abundance than both April periods ($P < 0.001$); January did not differ from the other periods.

The relationship between frequency of occurrence of all feeding sign combined and squirrel uncorrected density was significant for all periods except August 1997 (Table 6). The slopes of the regressions differed among periods for occurrence on 1-m^2 plots (ANCOVA; $F = 13.1$; $df = 4,4$; $P < 0.001$), as the 2 April periods differed from the other 3, but not each other. When pooled, the relationship for the April periods was strong ($r^2 = 0.901$, $P < 0.001$, $n = 15$) (Fig. 9) and exhibited narrow squirrel density prediction intervals (Fig. 10).

The incidence of type I and II errors among the pairwise comparisons of significance between study sites for April frequency of occurrence was 12.2% (6.1% each for type I and II errors). All errors were associated with the Clints Well study site, where we consistently had difficultly in obtaining reliable estimates and narrow confidence intervals.

Nest Counts. We counted 1.3-8.0 total and 0.6-2.7 active nests/km of line transect, with a mean of 4.3 (±0.8) total nests and 1.3 (±0.3) active nests/km (Table 8). Active nests constituted 30.7% of total nests observed. Nest density estimates ranged from 0.5 to 1.9 total nests/ha, and 0.1 to 0.6 active nests/ha (Table 8).

Number of total nests differed significantly among the 5 observers (Friedman ANOVA, $\chi^2 = 8.3$, $P = 0.003$, $n = 80$), with the differences attributed to counts by only 1 observer (Friedman ANOVA, $\chi^2 = 8.73$, $P = 0.003$); with this observer excluded, total number of nests did not differ. Number of active nests differed among observers (Friedman ANOVA, $\chi^2 = 7.0$, $P = 0.008$, $n = 80$); counts by 3 observers differed (Friedman ANOVA, $\chi^2 = 6.2$-8.9, $P = 0.003$-0.013). Coefficients of concordance for observers were poor; 0.411 for total nests and 0.366 for active nests.

The relationship between total nest density and mean corrected squirrel density was significant ($r^2 = 0.590$, $P = 0.026$, $n = 8$). The relationship between active nest density and mean corrected squirrel density was not significant ($r^2 = 0.228$, $P = 0.231$, $n = 8$).

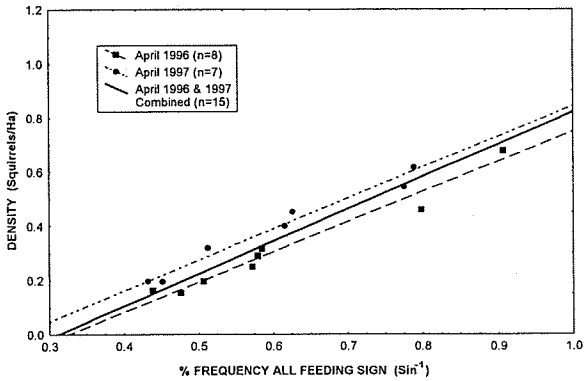


Figure 9. Regression of April tassel-eared squirrel uncorrected density/ha and percent frequency of occurrence of all feeding sign on 1-m^2 plots (sin^{-1} transformed) at 8 north-central Arizona study sites. Lines represent April 1996-97 combined, and 1996 and 1997 individually. Combined $r^2 = 0.901$, $P < 0.001$, $n = 15$.

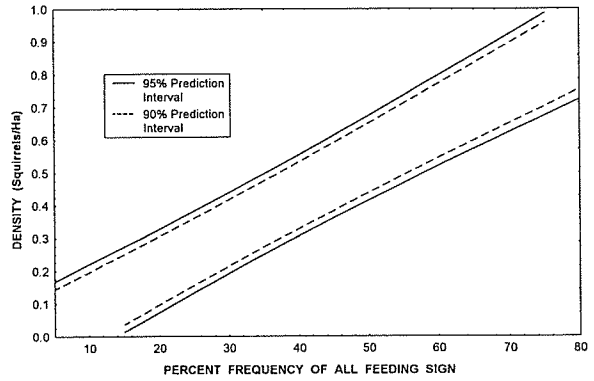


Figure 10. Prediction intervals (90% and 95%) around regression line for combined April 1996-97 tassel-eared squirrel uncorrected density/ha and percent frequency of occurrence of all feeding sign on 1-m^2 plots, derived from 8 north-central Arizona study sites.

Combined Index Techniques. In order to better predict squirrel density, we included the 2 indices that had the strongest (based on r^2 values) and most consistent (year-to-year) relationship to uncorrected density in a multiple regression analysis; the April and August periods were analyzed separately. For the April analysis, we assessed the relationships between track station counts and combined feeding sign counts on 1-m^2 plots with uncorrected squirrel density. This

Table 8. Results of tassel-eared squirrel nest counts conducted in September 1997 at 8 study sites in north-central Arizona, including number of total and active nests observed along transects, nests/ha, ±standard error, and 95% confidence intervals.

	Total squirrel nests				Active nests			
Study site	No. Nests	Nests/ha	SE	95% CI	No. nests	Nests/ha	SE	95% CI
Clints Well	25	0.79	±0.18	0.40 - 1.24	5	0.16	±0.07	0.06 - 0.43
Ft. Tuthill	25	0.60	±0.19	0.31 - 1.18	5	0.12	±0.05	0.04 - 0.31
Gash Flat	21	0.80	±0.19	0.50 - 1.30	8	0.21	±0.07	0.11 - 0.42
Long Valley	17	0.73	±0.28	0.33 - 1.60	3	0.06	±0.04	0.01 - 0.29
Marshall Mesa	39	1.86	±0.23	1.43 - 2.42	12	0.43	±0.13	0.23 - 0.81
Mormon Lake	9	0.53	±0.21	0.23 - 1.20	4	0.16	±0.10	0.04 - 0.64
Parks	46	1.37	±0.24	0.93 - 2.01	19	0.57	±0.17	0.31 - 1.06
Pumphouse	56	1.92	±0.44	1.18 - 3.13	17	0.49	±0.20	0.20 - 1.17
Mean	29.75	1.07	±0.25	--	9.12	0.27	±0.10	--

relationship was strong ($r^2 = 0.966$, $P < 0.001$, $n = 15$), but accounted for only 6.5% and 3.1% additional variance in squirrel density over feeding sign and track counts alone, respectively. Beta values for both independent variables were significant (feeding sign beta = 0.408, $P = 0.008$; track count beta = 0.597, $P < 0.001$).

For the August analysis we used the relationship between track station and cone core feeding sign on 1-m^2 plots with uncorrected density. Here, the ability to predict squirrel density improved when both indices were included ($r^2 = 0.786$, $P < 0.001$, $n = 15$). This analysis explained 25.4% more variance in uncorrected squirrel density than track counts alone and 8.9% more than cone sign alone. However, only 1 of the independent variable beta values was significant (track count beta = 0.562, $P = 0.047$; cone sign beta = 0.362, $P = 0.179$).

Track Count Power Analysis

Mean regression r^2 for April track station hits versus squirrel density increased from 0.660 for a 4 X 4 grid to 0.919 for a 9 X 9 grid at $\alpha = 0.05$, and from 0.653 for a 4 X 4 grid to 0.922 for a 9 X 9 grid at $\alpha = 0.10$. An asymptote occurred at grid sizes of 7 X 7 to 8 X 8 stations (Appendix 3, Fig. 11a). For random lines, mean r^2 ranged from 0.737 for 2 lines to 0.928 for 9 lines at $\alpha = 0.05$, and from 0.743 for 2 lines to 0.926 for 9 lines at $\alpha = 0.10$. The asymptote occurred at 7 lines (Appendix 3, Fig. 11a).

We found that reduced-effort designs yielded differing levels of power. With the full 10 X 10 grid, prediction intervals for April track count data overlapped to the degree that power to detect differences between low versus medium and medium versus high track counts was poor. Reduced-effort designs resulted in even lower power (Appendix 3). Power to detect differences in low versus high track counts ranged from 0.4% for a 4 X 4 grid to 78.9% for a 9 X 9 grid at $\alpha = 0.05$, and from 3.5% to 99.0% at $\alpha = 0.10$ (Fig. 11b). Power peaked at an 8 X 8 grid, regardless of α level (Fig. 11b).

Power to detect differences between low and high track counts for reduced effort random lines slightly outperformed grid designs (Appendix 3, Fig. 11b). Power ranged from 1.6% for 2 lines to 89.7% for 9 lines at $\alpha = 0.05$, and from 10.7% for 2 lines to 99.7% for 9 lines at $\alpha = 0.10$. An asymptote occurred at 7 lines for both α levels (Fig. 11b). Appendix 3 includes beta and intercept values necessary to construct design-specific regression prediction equations.

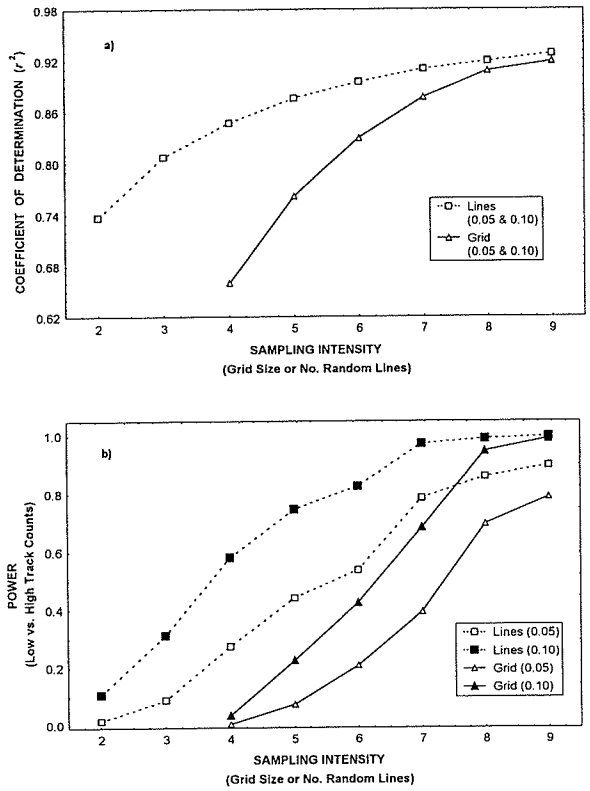


Figure 11. Bootstrap power analysis of reduced-effort sampling designs (grid versus random lines) for combined April 1996 and 1996 tassel-eared squirrel track station hits for 8 north-central Arizona study sites: a) mean coefficients of determination (r^2) by sampling intensity and type and b) power to detect differences between low and high track counts by sampling intensity and type.

Index Technique Evaluation

We employed the reduced-effort 8 X 8 grid design derived from the track count power analysis to conduct track and feeding sign (256 1-m^2 plots associated with the 8 X 8 grid design) counts at Camp Navajo and Mount Trumbull. Squirrel density estimates derived from 3 techniques (2 individual indices plus a combined track and feeding sign index; Table 9) did not differ significantly. Mean prediction interval widths among the 3 techniques were different (ANCOVA; $F = 431.8$; $df = 2,14$; $P < 0.001$) (Table 9), and all multiple comparisons were significant ($P < 0.001$). The mean prediction interval for the feeding sign technique was the widest (±0.10 squirrels/ha), while that for the combined track station and feeding sign technique was the narrowest (±0.07 squirrels/ha). Most of the sites we indexed supported relatively low squirrel densities (<0.15 squirrel/ha).

We detected no significant differences among observers for track counts or feeding sign counts at either Camp Navajo or Mount Trumbull. Furthermore, the results between areas were consistent. At Camp Navajo, the coefficient of concordance was 0.674 for track counts and 0.784 for feeding sign counts. At Mount Trumbull, the coefficient of concordance was 0.732 for track counts and 0.875 for feeding sign counts. The mean coefficient of concordance was 0.703 for track station counts compared to 0.830 for combined feeding sign counts. The greatest source of observer disagreement during track counts was identification of rock squirrel versus tassel-eared squirrel tracks.

Labor costs associated with track station counts included layout (pacing and flagging) of grids, which typically took 1 person 6 hours once the location was selected. Another hour was spent preparing the track stations, 2 hours placing them out on the grid, and another 2 hours to pick up and read 2 days later. One person can install 3 sets of track stations on established grids in a day. Other costs associated with this technique include the track stations, plates, chalk, alcohol, and bait; total approximate cost of materials and supplies for stations for an 8 X 8 grid was $90 (Drennan et al. 1998).

Feeding sign counts are not limited to using established grids and could be conducted simply by pacing off plots, saving the expense of grid layout. Feeding sign counts associated with 256 1-m^2 plots (comparable to an 8 X 8 grid) were completed by 1 person in 4 hours. Two sites were covered per day without observer fatigue. Labor costs associated with simultaneously conducting track station and feeding sign counts on established grids exceeded that of feeding sign counts alone by approximately 3 hours (1 hour for track station preparation and 2 hours for pick up and reading). One person was still able to cover 2 sites per day using both techniques.

Our relative ranking of the various population index techniques evaluated during this study is presented in Table 10. Of the 9 techniques we evaluated, April frequency of combined feeding sign on 1-m^2 plots ranked the best, followed closely by April track counts. All other techniques either ranked well behind or received insufficient evaluation during the study to make definitive conclusions regarding efficacy.

Table 9. Tassel-eared squirrel index count results for 3 Camp Navajo Army Depot and 6 Mount Trumbull sites conducted April-May 1998. Results include comparison of squirrel density/ha and 90% prediction intervals for track station, feeding sign, and combined track station and feeding sign index techniques.

	Track station technique			Feeding sign technique			Combined track & feeding sign technique	
Evaluation site	Track "hits"	Squirrel density/ha	90% prediction interval	% freq. of occurrence	Squirrel density/ha	90% prediction interval	Squirrel density/ha	90% prediction interval
Camp Navajo								
Treatment- North	5	0.128	0.041-0.214	18.4	0.184	0.082-0.288	0.142	0.077-0.208
Treatment-West	5	0.128	0.041-0.214	16.4	0.161	0.058-0.266	0.132	0.067-0.198
Control	2	0.102	0.014-0.190	10.2	0.090	0.000-0.199	0.085	0.018-0.152
Mt. Trumbull								
Treatment-1	2	0.102	0.014-0.190	16.0	0.156	0.053-0.261	0.114	0.048-0.181
Treatment-2	5	0.145	0.050-0.231	14.4	0.138	0.033-0.243	0.133	0.068-0.199
Treatment-3	7	0.145	0.059-0.231	--	--	--	--	--
Control-1	3	0.111	0.023-0.198	--	--	--	--	--
Control-2	12	0.189	0.105-0.274	23.0	0.236	0.137-0.339	0.203	0.139-0.267
Control-3	3	0.111	0.023-0.198	--	--	--	--	--
Mean width of prediction interval around estimate (squirrels/ha)			±0.087			±0.103		±0.067

Table 10. Relative ranking evaluation of various tassel-eared squirrel density techniques relative to technique precision (r^2), type I and II error rates, consistency between years (regression slopes ANCOVA) and among observers (Friedman ANOVA and concordance), and labor costs (hours/site). Average rank considers all criteria for which a technique was ranked; overall rank lists techniques from best (lowest score) to worst.

			Consistency between:				
				Observers			
Census index technique	Precision-r^2	Type I & II errors	Years-ANCOVA	ANOVA	Concordance	Labor costs-(hrs/site)	Average ranking (overall rank)
Nest counts	8	5	N/A	3	3	5	4.80 (8)
Snow track counts	9	N/A	N/A	N/A	N/A	4	6.50 (9)
Track station counts:							
January	4	N/A	N/A	N/A	N/A	4	4.00 (6)
April	2	2	1	2	2	2	1.83 (2)
August	6	4	5	N/A	N/A	2	4.25 (7)
Feeding sign counts (1-m^2 plots):							
January fungi	3	N/A	N/A	N/A	N/A	2	2.50 (4)
April clippings	5	5	2	1	1	1	2.33 (3)
April combined sign	1	1	3	1	1	1	1.33 (1)
August cones	7	3	4	N/A	N/A	1	3.75 (5)

DISCUSSION

We developed reliable indirect squirrel population index techniques using known population estimates against which we calibrated these techniques. We found strong relationships between index counts and uncorrected squirrel densities during every trapping period. In January 1996, we obtained strong correlations between squirrel density and fungi dig frequency of occurrence on 1-m^2 plots. However, heavy snows in January 1997 precluded assessment of fungi feeding sign as a population index estimator that year. As a result of the poor performance of winter track station and snow track index counts [also reported by Ffolliott (1990)], we were unable to develop an effective winter index.

Consistent and strong relationships were found between cone core feeding sign and squirrel density. However, in addition to a high type II error rate, use of cone core feeding sign was confounded by other factors. The peak of cone feeding activity and sign deposition by squirrels occurred in late summer to early fall (Keith 1965, Stephenson 1975, States et al. 1988). However, cone cores that appeared fresh persisted through January and April before noticeable oxidation occurred on the portion of cone cores resting on soil or litter. Consequently, cone core presence beyond late summer-early fall may not reflect short-term squirrel density.

The non-uniform abundance distribution associated with 20-m^2 plots presented another problem with using cone core feeding sign, which apparently biased estimates of mean August cone core abundance. Though strong relationships were present for August cone core sign frequency of occurrence on 1-m^2 plots, prediction intervals were unacceptably wide, precluding meaningful squirrel density estimates.

Our attempts to combine cone core feeding sign and track station count data in a multiple regression analysis for late summer-early fall (corresponding to our August trapping periods) met with limited success. Though the relationship with density improved substantially, only 1 independent variable (tracks) was significant and the combined technique was still insufficient to yield prediction intervals suitable for management application. Therefore, we were unable to derive a reliable density index technique for the late summer-early fall period.

Our mean total nest density of 1.07 nests/ha was higher than densities reported by Farentinos (1972*b*) of 0.56 nests/ha, Patton (1975*a*) of 0.63 nests/ha, and Halloran and Bekoff (1994) of 0.47 nests/ha. Unlike our study, Patton and Wadleigh (1986) were unable to detect a significant relationship between total nests/ha and Kaibab squirrel density over 7 years. Patton (USDA For. Serv., unpubl. data) did find a significant relationship ($r^2 = 0.579$) between active nest and Abert squirrel density very similar to ours. Our nest index technique was costly, time consuming, and exhibited substantial observer bias and low concordance among observers.

Several reliable techniques were derived for spring use. The relationship between terminal clippings and uncorrected density provided a marginally acceptable technique in itself, but was surpassed by combined feeding sign and track station counts. We believe that the strong and consistent relationships of both frequency of occurrence of combined feeding sign and track station counts with April uncorrected densities were attributable to limited food quantity and quality during and immediately following winter (Keith 1965, Brown 1984, States et al. 1988, Allred et al. 1994). Despite annual variation in snowfall, squirrels still relied on terminal clippings in the spring, comprising up to 85% of their feeding activity (States et al. 1988). The effectiveness of baited track stations may likewise reflect unavailability of preferred foods, particularly compared to August, when food abundance and quality typically was at its peak (Keith 1965, Stephenson 1975, States et al. 1988). The apparent improvement in correlation and predictive power between April clippings alone and feeding sign combined may reflect a density-dependent sensitivity to fungi digs and recovered buried cones (States et al. 1988).

Of the 2 April index techniques, counts of combined feeding sign ranked the best. This technique particularly outperformed track station counts in its ability to detect differences in populations with type I and II error rates <15%. Combined feeding sign counts also had lower associated costs than did track station counts. Track station counts may be especially useful in

pre- and post-treatment studies where an established grid design is desired.

The bootstrap power analysis of April track station count data indicated low power to discriminate between low and medium, and medium and high track counts. Similar analysis needs to be conducted for April combined feeding sign frequency of occurrence on 1-m^2 plots. By combining the 2 spring techniques, sufficient power may be attained to detect differences in low versus medium and medium versus high squirrel densities. Our multiple regression analysis incorporating both combined feeding sign and track station counts versus uncorrected density accounted for only a nominally increased explanation of variance in squirrel densities above individual simple regressions. Yet, squirrel density prediction intervals narrowed significantly compared to the 2 individual techniques. Average squirrel density prediction intervals for tracks and feeding sign combined for the Camp Navajo and Mount Trumbull evaluation sites were 35.0% narrower than estimates from feeding sign alone and 23.0% narrower than tracks alone. Along with the significance of both independent variables in the multiple regression model and narrowed prediction intervals, increased power may be attained under a combined technique once a power analysis similar to that done for track counts is accomplished.

Even though the track station power analysis exposed limitations in comparing low to medium and medium to high track counts, it nonetheless helped identify reduced-effort sampling designs that optimized effort, precision, and power. The options of using an 8 X 8 grid or 7 random lines are available, but the grid has advantages over random lines. A grid requires fewer track stations (64 versus 70). The 24 ha required to accommodate the 8 X 8 grid is considerably smaller than the 40 ha for a 10 X 10 grid required to randomly select and orient 7 lines. For these reasons, an 8 X 8 grid best optimizes effort, precision, power, and logistical considerations in estimating squirrel density.

CHAPTER III

RELATIONSHIPS OF TASSEL-EARED SQUIRREL POPULATION DYNAMICS AND FOREST HABITAT STRUCTURE

METHODS

Habitat Assessment

Habitat Measurements. We measured habitat characteristics previously reported to affect tassel-eared squirrel populations (Ratcliff et al. 1975; Pederson et al. 1976, 1987; Patton 1984) and pertinent to forest management. At each study site, 25 of the interior 100 trapping stations (Fig. 4) were randomly selected. Then, a 0.10 ha circular plot was located in a random direction and distance ≤35 m from the trapping station point. Habitat variables were measured during fall 1997 while deciduous species were still leaved.

Within each plot, we measured diameter at breast height (dbh) for all pine and gambel oak ≥2.5 cm dbh and juniper diameter at root crown (drc) ≥2.5 cm. We counted all live trees and shrubs <2.5 cm dbh/drc and ≥1 m in height on the plots by species.

We estimated canopy cover by vertical projection, using a staff-mounted, self-leveling sighting periscope (Ganey and Block 1994). Observers recorded periscope cross hair interceptions with canopy foliage >2 m height at 100 points. Sighting points were located every 1.2 m along 4 transects (15 points/transect) emanating from the plot center in cardinal directions (n = 60). Additional points (n = 40) were located every 2.4 m along 4 transects (10 points/transect) forming a square within the outer perimeter of the plot (Fig. 4). We measured the relative incidence of trees with "interlocking" canopy crowns ≤1.5 m of each other, which was the distance we observed squirrels readily jumping from tree to tree. We counted continuously interlocking canopy trees >15 cm dbh starting from the closest tree at each of 5 points; 1 at the plot center and 1 each at the end of the 4 cardinal transects (Fig. 4).

Four habitat variables were calculated from overstory tree measurements for each sampling plot and averaged for each study site: 1) stand density index (SDI), 2) quadratic mean diameter (D_q) by tree species, 3) basal area by tree species, and 4) tree density corresponding to vegetation structural stage (VSS) classes. Raw SDI values were computed only for pine using an exponent factor of 1.605 (McTague and Patton 1989). We calculated tree density by VSS diameter class (Reynolds et al. 1992): VSS 2 (2.5-12.5 cm dbh), VSS 3 (12.6-30.3 cm dbh), VSS 4 (30.4-45.6 cm dbh), VSS 5 (45.7-61.0 cm dbh), and VSS 6 (>61.0 cm dbh). Mean values are reported ± standard error.

Habitat Gradient Analysis and Ordination. We used principal components analysis (PCA) to ordinate the 8 study sites along gradients of habitat structural condition. We retained those principal component axes that accounted for significant variation in the habitat variables. Each axis reflected an orthogonal (independent) habitat gradient derived from correlations with habitat variables and represented the best linear fit of correlated variables. PCA scores for the first 3 axes were used to construct an ordination diagram depicting relative positions of the 8 study sites in multidimensional habitat space.

Habitat and Squirrel Population Relationships

We assessed relationships of tassel-eared squirrel uncorrected and corrected density, survival, recruitment, fitness, and nest (total and active) density to 13 study site habitat structural characteristics (see Tables 11-13 for list of habitat variables) using Spearman rank correlations (r_s). We also related habitat variables to the mean change in squirrel uncorrected density from April to August to assess the influence of habitat structure on seasonal fluctuations. We evaluated relationships between squirrel population response variables and the 4 PCA factors that accounted for significant variation in the habitat structural characteristics (Morrison et al. 1992). We recognized that conducting the large number of regression analyses (8 population variables X 17 habitat variables = 136 regressions) from the same data sets may result in spurious results of significance (Rice 1989). To address this problem we applied a sequential Bonferroni test for significance (Rice 1989), correcting for multiple regressions done for each population variable data set (17 comparisons).

RESULTS

Habitat Assessment

Habitat Measurements. Habitat structural characteristics varied greatly among study sites (Table 11, Fig. 12). Ponderosa pine influenced study site overstory habitat characteristics the most (Table 11, Fig. 12), though Gambel oak also was prevalent at some study sites (Table 12). Small tree and shrub values varied greatly among sites (Tables 11 and 12); 5 sites had minimal understory, 2 had substantial ponderosa pine understory, and 1 had a prevalent understory of New Mexican locust.

Habitat Gradient Analysis and Ordination. Our PCA analysis reflected the high variation in habitat structure among study sites and separated 4 principal components (factors). These 4 factors accounted for 81.5% of the total variance in the original data (Table 13). The ordination diagram reflects the relative positions of the 8 study sites in multivariate habitat space for the first 3 PCA factors, accounting for 70.7% of total variation (Fig. 13).

PCA Factor 1 accounted for 31.6% of total variance and was influenced primarily by ponderosa pine SDI, percent canopy closure, and basal area (Table 13). Therefore, a low or negative value for Factor 1 indicated sites with low SDI, canopy closure, and basal area; i.e., Ft. Tuthill, Long Valley, and Pumphouse study sites (Fig. 13).

Factor 2 explained 21.5% of the total variance and described D_q and VSS 3 and VSS 6 diameter class tree density (Table 13). This factor put the Pumphouse study site at 1 end of the spectrum and Clints Well at the opposite end; other sites fell in between (Fig. 13). Mean D_q for Clints Well was substantially lower (16.5 cm) than the other 7 sites ($\bar{x}$ = 32.1 cm) because of the large number of VSS 2 diameter class trees (1619 stems/ha ±228.8), compared to other study sites ($\bar{x}$ = 38.3 stems/ha ±9.0).

Factor 3 described VSS 2 and VSS 4 diameter class density, D_q, and number of interlocking canopy trees, accounting for 17.7% of total variance (Table 13). PCA ordination of Factor 3 put the Parks study site at 1 end of the spectrum (low VSS 2, and high VSS 4, D_q, and interlocking canopy). Clints Well again fell at the opposite end of the spectrum (Fig. 13).

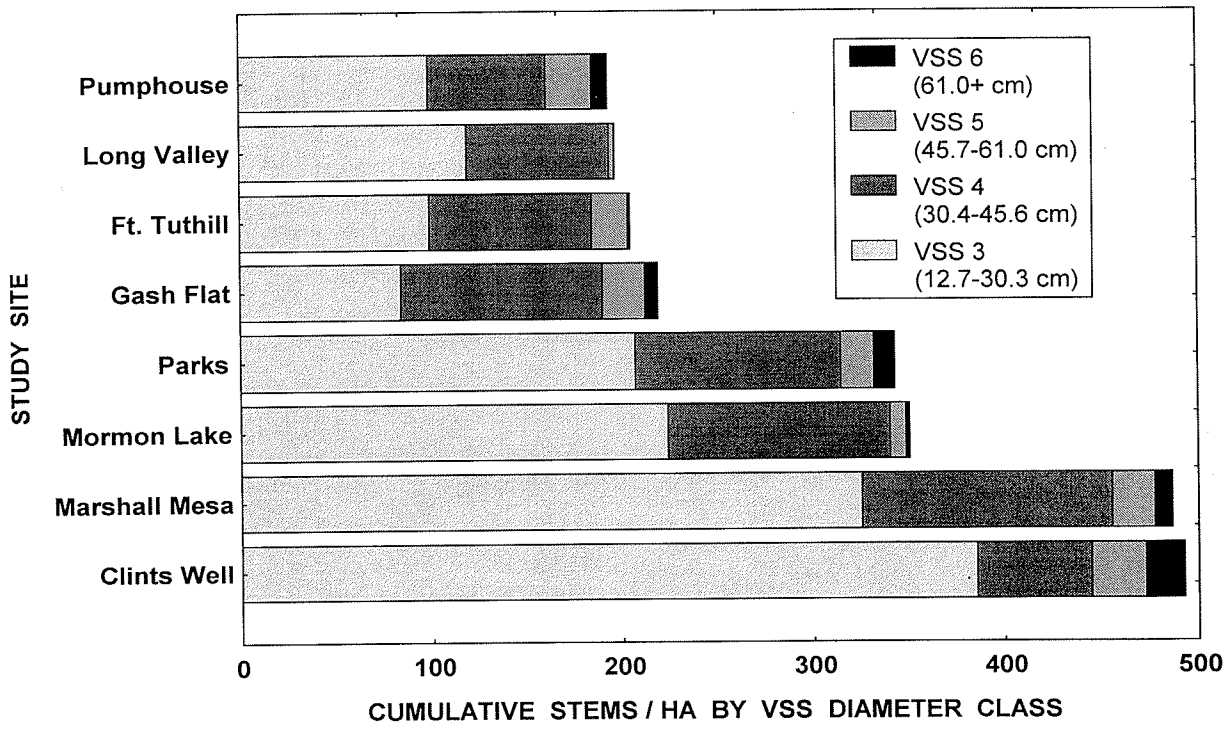


Figure 12. Cumulative tree stems/ha by vegetative structural stage (VSS) diameter class (VSS 3-6) for 8 north-central Arizona study sites. Data collected in 1997.

Table 11. Habitat characteristic mean values ±standard error and observed sample ranges for 8 study sites in north-central Arizona sampled in 1997; BA = basal area, D_q = quadratic mean diameter, SDI = standard density index.

Study site	All trees/ha >2.5cm dbh ±SE	Pine trees/ha <2.5cm dbh ±SE	BA (m^2/ha) ±SE	$D_q$cm ±SE	SDI ±SE	% Canopy closure ±SE	Interlocking trees/point ±SE
Clints Well	2,112.00 ±233.40	543.20 ±101.73	39.83 ±6.06	16.48 ±1.12	373.48 ±44.98	59.40 ±2.45	3.71 ±0.24
Ft. Tuthill	226.00 ±37.50	40.12 ±11.12	16.21 ±1.06	32.84 ±1.24	119.30 ±9.33	31.60 ±2.01	2.23 ±0.19
Gash Flat	276.00 ±29.23	259.62 ±67.50	22.14 ±1.52	32.64 ±1.04	156.38 ±11.25	38.84 ±2.37	3.63 ±0.19
Long Valley	268.57 ±28.42	8.80 ±5.39	16.81 ±2.06	27.91 ±0.96	128.50 ±15.01	27.50 ±3.35	2.77 ±0.18
Marshall Mesa	603.60 ±36.04	43.60 ±5.89	57.71 ±16.78	31.72 ±3.53	373.48 ±78.59	52.68 ±2.86	4.92 ±0.22
Mormon Lake	363.60 ±27.75	6.00 ±2.70	24.81 ±3.48	29.03 ±1.32	183.89 ±20.27	38.64 ±1.84	3.49 ±0.16
Parks	353.20 ±48.05	12.00 ±4.08	26.82 ±2.36	36.20 ±2.59	194.60 ±18.62	47.48 ±3.58	4.18 ±0.35
Pumphouse	225.20 ±24.25	29.20 ±5.73	18.22 ±1.71	34.65 ±1.93	131.12 ±12.06	37.40 ±3.01	2.65 ±0.21
Observed sample range	10.00 - 5,280.00	0.00 - 8,985.72	1.77 - 414.83	9.17- 91.69	14.58 - 2,000.68	1.00 - 83.00	0.40 - 7.20

Table 12. Density (trees/ha) and basal area (m^2/ha) ± standard error for non-ponderosa pine live trees ≥2.5 cm dbh, and small tree and shrub (<2.5 cm dbh and >1 m height) density measured in 1997 at 8 study sites in north-central Arizona.

Study site	Tree/shrub species	Trees/ha ≥ 2.5 cm dbh	±SE	Trees≥2.5 cm dbh BA (m^2/ha)	±SE	Small trees <2.5 cm dbh & shrubs/ha	±SE
Clints Well	Gambel oak	31.60	±10.13	0.61	±0.08	2.39	±0.45
	Juniper	4.00	±1.28	0.08	±0.02	2.39	±0.45
Ft. Tuthill	New Mexican locust	--	--	--	--	293.19	±81.21
Gash Flat	Gambel oak	58.00	±31.02	2.37	±0.52	38.83	±10.10
Long Valley	--	--	--	--	--	--	--
Marshall Mesa	Gambel oak	50.80	±6.71	2.67	±0.42	--	--
	Juniper	61.59	±8.13	1.72	±0.27	9.20	±1.24
Mormon Lake	Gambel oak	48.80	±13.73	1.02	±0.25	35.60	±16.02
Parks	--	--	--	--	--	--	--
Pumphouse	Juniper	--	--	--	--	0.80	±0.15

Table 13. Principal component analysis (PCA) factors describing habitat characteristics measured in 1997 at 8 study sites in north-central Arizona. Values are correlation coefficients between original variables and individual components. Asterisks indicate variables exhibiting greatest influence on each PC factor.

	PCA Correlation Coefficients			
PCA Habitat Variable	Factor 1	Factor 2	Factor 3	Factor 4
Basal area (m^2/ha)	0.23*	0.24	-0.13	0.32*
Quadratic mean diameter	-0.03	0.36*	-0.30*	0.01
Standard density index	0.27*	0.18	-0.04	0.27*
No. VSS 2 stems/ha	0.16	-0.03	0.43*	0.04
No. VSS 3 stems/ha	0.20	-0.27*	0.08	0.26
No. VSS 4 stems/ha	0.08	-0.21	-0.39*	-0.01
No. VSS 5 stems/ha	0.10	0.13	0.03	-0.74*
No. VSS 6 stems/ha	0.14	0.25*	0.20	-0.16
Canopy closure (%)	0.26*	-0.17	-0.03	-0.28*
No. interlocking canopy trees/point	0.16	-0.13	-0.28*	-0.21
% total variance explained	31.6	21.5	17.7	10.7
% cumulative variance explained	31.6	53.1	70.8	81.5

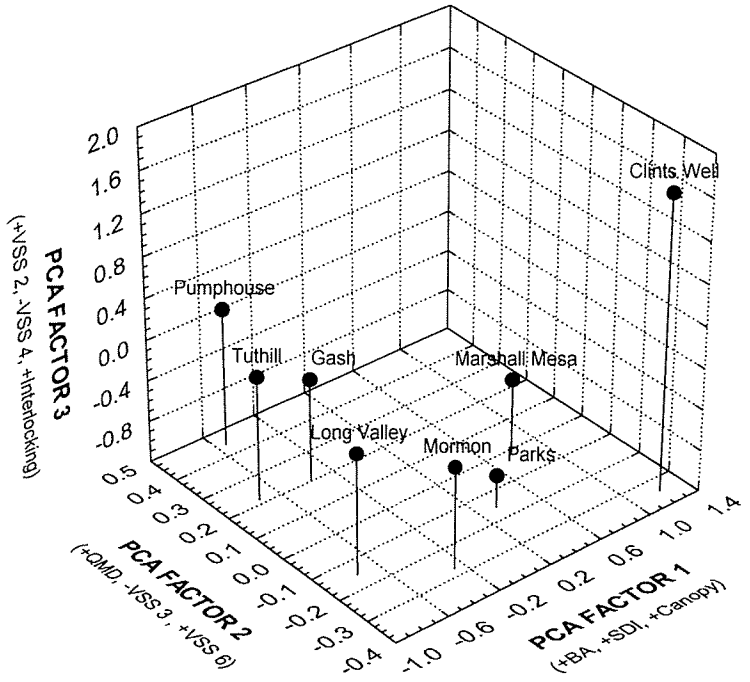


Figure 13. Principal components analysis (PCA) ordination of habitat characteristics for 8 north-central Arizona tassel-eared squirrel study sites. Ordination diagram reflects mean study site scores for the first 3 components (factors) describing 71% of total variance. Components describe: basal area, SDI, canopy closure (PCA 1), quadratic mean diameter, density of VSS 3 and 6 diameter trees/ha (PCA 2), and number of VSS 2 and 4 diameter trees/ha and no. interlocking canopy trees (PCA 3). Habitat assessment conducted in 1997.

PCA Factor 4 explained 10.7% of the total variance and described VSS 5 diameter class density, along with basal area, canopy closure, and SDI (Table 13).

Habitat and Squirrel Population Relationships

Spearman rank correlation analysis of 13 individual study site structural habitat variables and the 4 PCA factors with squirrel population variables and nest density yielded only 3 significant relationships following sequential Bonferroni testing. No relationships between habitat structural variables and uncorrected or corrected squirrel density, survival, and nest density were significant. Also, no regressions between the 4 PCA factors and squirrel population variables were significant.

The mean fluctuation change in uncorrected squirrel density from April to August was significantly related to D_q ($r_s = 0.881$, $P = 0.003$, $n = 8$). Mean squirrel recruitment was highly related to the number of interlocking canopy trees ($r_s = 1.000$, $P < 0.001$, $n = 7$). Mean squirrel fitness was highly related to tree basal area ($r_s = 0.919$, $P = 0.003$, $n = 7$).

DISCUSSION

Based on PCA ordination, we achieved our objective to orient study sites across a gradient of structural habitat conditions. We considered multiple squirrel population response variables, including survival, recruitment, and fitness to assess habitat quality (Van Horne 1983). The role and significance of forest patchiness and interlocking canopy became apparent only when we considered squirrel population response variables besides density.

As discussed in Chapter I, we suspected that peak uncorrected density observed during late summer at some study sites was related to the availability of pine cones. Keith (1965), Hall

(1981), and Patton et al. (1985) found that cones played a role in tassel-eared squirrel population fluctuations, and Buchanan et al. (1990) related high densities of Douglas squirrels (*Tamiasciurus douglasii*) to cone availability. Larger trees in the 30-74 cm dbh range were particularly important for squirrel cover and food (Patton et al. 1985). Some of our sites which would otherwise be considered structurally marginal (Pederson et al. 1976, 1987; Patton 1984, Patton et al. 1985) seasonally provided quality food and supported high squirrel densities, possibly tied to the density of larger cone producing trees. We found that mean uncorrected density fluctuations were positively related to D_q, and Larson and Schubert (1970) reported that pine cone production and crop frequency were positively related to tree diameter. Patton et al. (1985) reported a significant positive correlation between squirrel density and D_q.

Pederson et al. (1987) and Patton et al. (1985) reported on the importance of overstory tree clumpiness and canopy closure. However, an "index of patchiness" could not be significantly correlated with squirrel density (Patton 1975*b*). No such relationship existed between clumpiness or canopy closure and squirrel density in our study. Our strongest relationship occurred between number of interlocking canopy trees and squirrel recruitment. Study sites that had undergone heavy even-aged timber harvest and had less than 3 interlocking trees per sample point exhibited minimal or inconsistent squirrel recruitment. Patton (1975*a*) reported that 92% of nests were found in trees growing inside a group, with 75% having 3 or more interlocking canopy trees.

The relationship between squirrel fitness and basal area provided insight into potential effects of forest management practices on tassel-eared squirrels. Past studies found basal area important to tassel-eared squirrels. Ratcliff et al. (1975) found a significant relationship between squirrel density and basal area. Pederson et al. (1987) and Patton et al. (1985) reported lower squirrel density, recruitment, and preferred food (hypogeous fungi) associated with reduced basal area, canopy closure, and tree density. States and Gaud (1997) also reported on reduced fungi production in association with reduced basal area.

Our relationship between squirrel fitness and basal area suggests that a threshold effect may exist. Only 1 of our study sites, Marshall Mesa, exhibited fitness exceeding the mean for all 8 sites. In spite of our efforts to orient study sites along a gradient of habitat condition and squirrel density, only Marshall Mesa had a combination of moderate-high density, survival, and recruitment under drought conditions. Uncertainty exists over whether a threshold effect between squirrel fitness and basal area is biologically meaningful or simply an artifact of our sampling design, where intermediate and other upper points were lacking. Patton's (1984) model of tassel-eared squirrel habitat capability (density) and habitat quality exhibited an exponential fit, also suggesting a threshold effect. His model had only 1 case oriented at upper levels of his curve. Patton (1984:412) nonetheless concluded that "the regression line is a reasonable assumption...(since)...optimum habitats likely do not exist in many areas due to the intensity of timber harvesting in the past." This conclusion preceded an era of unprecedented intensity of timber harvest in Arizona (mid-1980s to early 1990s) that reduced squirrel habitat quality. For 1 national forest in Arizona, squirrel habitat capability was projected by modeling to decline an average of 20% on 40 timber sales (Dodd and Adams 1989). As early as the 1960s, Keith (1965:161) expressed concern relative to timber impact on tassel-eared squirrels, reporting that "the long-term decrease in squirrel populations is probably related to logging of ponderosa pine.....without a doubt this intensity of logging seriously deteriorated Abert squirrel habitat."

Forest management can improve squirrel habitat through creation of suitable habitat conditions and spatial arrangement of different habitats (Ffolliott and Patton 1975, Patton 1984). For instance, our study documented seasonal use of intensively thinned areas by squirrels apparently tied to pine cone seed availability. Widespread even-aged forest management has reduced stand, patch, and landscape diversity (Patton 1992). It is desirable to accommodate the requirements of a wide variety of forest-dwelling species, including tassel-eared squirrels. This can best be accomplished by providing for a diverse arrangement of structural habitat conditions and patch sizes (Patton 1992).

There has been a trend since the mid-1980s

toward reducing stand sizes, such that openings and stands have become similar in size. Therefore, homogeneity has been increased at a landscape scale (Arizona Game and Fish Department 1993*a*). This homogenization remains an issue under current forest restoration practices (Covington and Fule 1995) and northern goshawk management guidelines (Reynolds et al. 1992). Concern exists that forest management activities may diminish remaining high quality squirrel population source areas, which produce surplus squirrels for emigration to dispersal sinks. If our basal area relationship is biologically meaningful, it may reflect a threshold where further wide-scale reduction of squirrel habitat structural attributes and landscape diversity impact squirrel population and genetic viability.

CONCLUSIONS AND MANAGEMENT OPTIONS

We documented a wide range of tassel-eared squirrel densities across our 8 study sites. Uncorrected densities for most sites fluctuated greatly from season to season, but densities corrected for edge effect were comparatively stable. Mean recruitment was low, probably attributable to severe drought conditions, while average survival was high. Neither recruitment nor survival contributed substantially to seasonal fluctuations in densities. Seasonal density fluctuations most likely reflected a complex relationship between seasonally expanded home ranges by adjacent squirrels and squirrel immigration from higher quality source areas into lower quality dispersal sinks. In either case, squirrels were using seasonally available cone crops at sites where timber harvest thinning probably promoted cone production.

Our study pointed to the importance of overstory patchiness and interlocking canopy trees to tassel-eared squirrel recruitment. Squirrel fitness was positively related to tree basal area, and the relationship suggests that a threshold exists between basal area and maintenance of tassel-eared squirrel fitness. As forest health initiatives and northern goshawk management guidelines are pursued, managers must be cognizant of tassel-eared squirrel landscape habitat needs, particularly where habitat thresholds have the potential to be crossed.

Successful development of population index techniques provides the means to efficiently assess tassel-eared squirrel densities among years, across landscapes, and in response to forest treatments. The index techniques we developed are applicable only to the spring-early summer period when preferred squirrel foods are limited. We were unsuccessful in developing reliable index techniques for application during the winter and late summer-fall periods.

Winter proved to be the most limiting period for squirrel survival, and survival during this period was significantly lower than all other periods. Though direct assessment of sport hunting impact on squirrel populations was a minor component of this study, we found that non-juvenile squirrel survival through the fall hunt period exceeded the study average. Hunting did not appear to limit squirrel populations on our study sites.

Tassel-eared squirrels are a visible and integral component of Arizona's ponderosa pine ecosystems. They provide a window for us to better understand complex relationships with other ecosystem components. Our efforts contributed to an improved understanding of tassel-eared squirrel ecology and management that should allow managers to better balance forest restoration with habitat requirements.

Management Options

Tassel-eared squirrel habitat in Arizona has been altered by forest management practices that have reduced the mature tree forest component, clumpiness, and patch size, while increasing forest homogeneity and fragmentation. Incorporation of the following options into all forest management plans will maintain squirrel source populations and promote improvement of degraded habitats. Failure to incorporate these prescriptions may contribute to declines in tassel-eared squirrel populations. Options for application of tassel-eared squirrel population index techniques and for habitat management include:

1. Where resources allow, squirrel density index technique application should include both combined feeding sign frequency of occurrence (on 1-m^2 plots) and track station counts. Until more refined guidelines are developed, index counts should:

    a. Utilize an 8 X 8 grid size with 70 m spacing, including 64 track stations and 256 1-m^2 feeding sign plots.

    b. Where only a single technique can be used, the spring combined feeding sign technique is preferred.

    c. Specific guidelines for identifying, counting, and analyzing squirrel feeding sign and tracks should be obtained from the senior author.

2. Forest structural habitat variables were found to be positively correlated with squirrel population response variables at the stand scale. Stand-scale habitat parameters (associated with sites that exhibited average or above recruitment) that merit special attention during forest management and future research activities include:

   a. Areas exhibiting high tree basal area [>35 m^2/ha (150 ft^2/ac)], especially where larger VSS 4 and 5 trees are present, should be maintained where possible. Where forest treatments are planned, applying a variable thinning prescription with a range of tree basal areas retained within and between harvest areas will benefit squirrels.

   b. Because of the importance of interlocking canopy trees to squirrel recruitment, thinning of overstory trees in stands exhibiting canopy clumpiness and interlocking crowns in such a manner as to retain these characteristics will benefit squirrels. Clumps of >5 interlocking canopy trees >15 cm (6 in) dbh with canopies ≤1.5 m (5 ft) together should be interspersed throughout stands in a variable spacing regime. Study sites with at least average levels of recruitment had a minimum of 22 patches/ha (9 patches/ac), which we consider important to maintaining squirrel populations. Where lacking, forest treatments should accommodate enhancement of canopy clumpiness and interlocking canopy trees to improve squirrel habitat.

   c. Larger trees in the VSS 5 and 6 diameter classes typically occur in a deficit relative to the desired distribution (Reynolds et al. 1992). To enhance squirrel populations, maintenance of >20 trees/ha (8 trees/ac) in the VSS 5 diameter class and adequate numbers of VSS 4 trees [>125 stems/ha (50 stems/ac)] should be retained during forest management activities.

3. Forest management activities must consider landscape-scale habitat relationships in addition to stand-scale habitat needs of squirrels. Important higher quality source habitats for squirrels may be limited in distribution and abundance. Source areas exhibit these characteristics:

   - basal area >35 m^2/ha (150 ft^2/ac)
   - VSS 5 diameter class tree density >20/ha (8/ac)
   - SDI >250
   - D_q >31 cm (12 in)
   - >22 patches/ha (9/ac) of >5 interlocking canopy trees.

4. In future assessments of squirrel habitat quality, all population parameters that contribute to squirrel fitness should be measured, including density, survival, and recruitment. Considering squirrel density alone may not be reflective of habitat quality (Van Horne 1983).

Research Needs

Future studies should focus on priority research needs identified in the project problem analysis (Brown 1995). Additional questions raised during the course of our study related to squirrel population dynamics, index techniques, and habitat relationships should also be addressed. Future research needs include:

1. Evaluation of landscape-scale tassel-eared squirrel population and habitat relationships, including:

   a. Habitat patch size, condition, and juxtaposition relationships associated with squirrel density, survival, reproductive biology, and dispersal patterns.

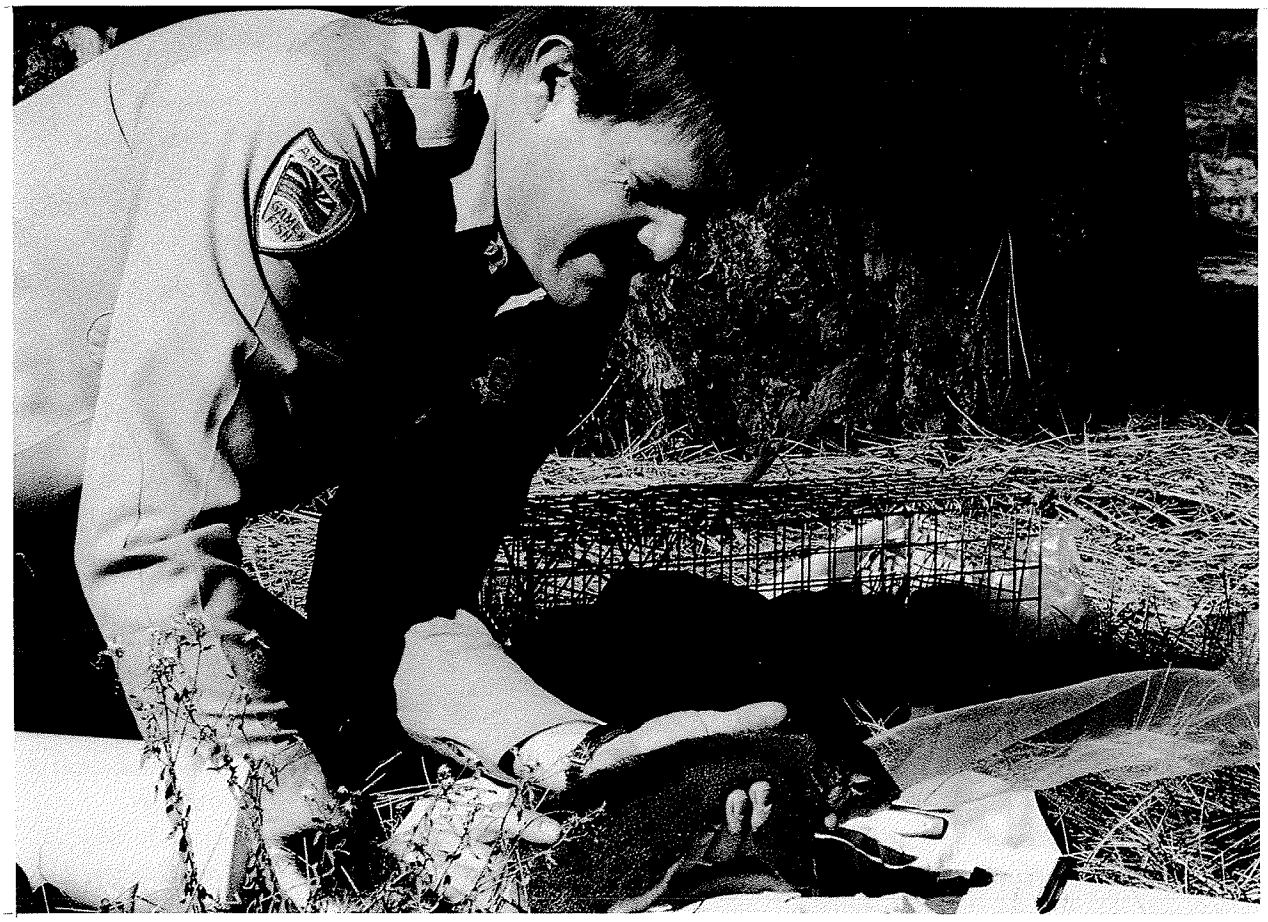
   b. Increased sampling of habitat stands within study area landscapes to provide for enhanced assessment of stand-level habitat needs (i.e., facilitating multiple regression analyses) and existence of habitat thresholds to maintaining squirrel fitness.

c. Further examination of squirrel habitat source and sink phenomena to improve our understanding of squirrel meta-population dynamics and provide refined options for forest management.

2. Further investigation of sport hunting impact on squirrel populations, including evaluation of the influence of roads, habitat condition, and hunter behavior impact on different age classes of squirrels.

3. Refine population index techniques for the spring period, incorporating an integrated power analysis for track station and combined feeding index techniques.

4. Validate refined index techniques, comparing predicted densities to known estimates derived from capture-recapture population estimation across a range of habitat conditions and squirrel densities.



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APPENDIXES

Appendix 1. Non-target species captured during 6 trapping periods 1996-97 at 8 study sites in north-central Arizona.

	Number of captures by capture-recapture trapping period						
Non-target Species	Jan 1996	Apr 1996	Aug 1996	Jan 1997	Apr 1997	Aug 1997	Total
Mammals:							
Golden-mantled ground squirrel (*Spermophilus lateralis*)	3	46	449	--	36	1,226	1,760
Rock squirrel (*S. variegatus*)	--	11	114	--	7	130	262
Striped skunk (*Mephitis mephitis*)	--	--	17	--	1	55	73
Mexican woodrat (*Neotoma mexicana*)	--	--	6	--	--	67	73
Chipmunk (*Tamias* spp.)	--	2	39	--	1	12	54
Ringtail (*Bassariscus astutus*)	--	--	2	--	--	11	13
Cottontail rabbit (*Sylvilagus* spp.)	--	--	7	--	--	1	8
Red squirrel (*Tamiasciurus hudsonicus*)	--	--	2	--	--	1	3
Gray fox (*Urocyon cinereogenteus*)	--	--	--	--	--	2	2
Porcupine (*Erethizon dorsatum*)	--	--	--	--	--	1	1
Birds:							
Steller's jay (*Cyanocitta stelleri*)	9	28	43	43	31	19	173
Dark-eyed junco (*Junco hyemalis*)	--	2	13	--	9	16	40
Acorn woodpecker (*Melanerpes formicivorus*)	--	3	--	--	1	1	5
Mountain chickadee (*Parus gambeli*)	--	--	--	--	--	1	1
Reptiles:							
Bull snake (*Pituophis melanoleucus*)	--	--	1	--	--	1	2
Totals	12	92	692	43	86	1,542	2,467

Appendix 2. Body weights of tassel-eared squirrels trapped during 6 capture-recapture trapping periods 1996-97, at 8 study sites in north-central Arizona.

Body weight range (g)	Frequency (%) of squirrel captures					
	Jan 1996	Apr 1996	Aug 1996	Jan 1997	Apr 1997	Aug 1997
400-450	0 (0.0)	0 (0.0)	1 (0.8)	2 (6.1)	0 (0.0)	0 (0.0)
451-500	2 (3.7)	0 (0.0)	3 (2.2)	3 (9.1)	0 (0.0)	0 (0.0)
501-550	6 (9.2)	1 (2.3)	5 (3.8)	6 (18.2)	2 (5.0)	1 (1.8)
551-600	2 (3.7)	8 (18.6)	17 (12.9)	3 (9.1)	2 (5.0)	4 (7.0)
601-650	11 (20.3)	14 (32.6)	29 (22.0)	1 (3.0)	6 (15.0)	5 (8.8)
651-700	9 (16.7)	12 (27.9)	42 (31.8)	2 (6.1)	8 (20.0)	18 (31.6)
701-750	14 (25.9)	41 (14.0)	25 (18.9)	8 (24.2)	15 (37.5)	18 (31.6)
751-800	7 (12.9)	1 (2.3)	10 (7.6)	4 (12.1)	3 (7.5)	10 (17.5)
801-850	4 (7.4)	1 (2.3)	0 (0.0)	3 (9.1)	4 (10.0)	0 (0.0)
851-900	0 (0.0)	0 (0.0)	0 (0.0)	1 (3.0)	0 (0.0)	1 (1.8)
No. squirrels	54	43	132	33	40	57
Mean weight[1]:						
All squirrels	665.7	645.3	644.0	627.9	685.6	690.0
Adult squirrels[2]	686.7	648.2	649.7	718.7	694.1	692.9

[1]Mean weights from original data.
[2]Squirrels ≥500 g in August, ≥550 g in January and April.

Appendix 3. Bootstrap analysis of April 1996-97 tassel-eared squirrel track station data for reduced-effort sampling designs (grids or random lines) of varying sizes and alpha levels. Summary includes mean coefficients of determination (r^2) ±standard error, power to detect differences between low versus medium, medium versus high and low versus high track numbers, and mean regression coefficients (Beta) and intercepts.

					Power to detect differences[1]			Regression equation:	
Design	Size	Alpha level	Mean r^2	Mean r^2 SE	Low vs. med	Med vs. high	Low vs. high	Mean beta	Mean intercept
Grid	4x4	0.05	0.660	±0.005	0.000	0.001	0.004	0.038	0.165
	5x5	0.05	0.762	±0.004	0.000	0.001	0.073	0.028	0.138
	6x6	0.05	0.829	±0.003	0.000	0.017	0.208	0.021	0.120
	7x7	0.05	0.877	±0.002	0.001	0.017	0.393	0.017	0.103
	8x8	0.05	0.908	±0.001	0.001	0.096	0.696	0.013	0.095
	9x9	0.05	0.919	±0.001	0.007	0.048	0.789	0.010	0.091
Grid	4x4	0.10	0.653	±0.005	0.000	0.000	0.035	0.037	0.167
	5x5	0.10	0.765	±0.004	0.000	0.013	0.226	0.028	0.137
	6x6	0.10	0.833	±0.003	0.001	0.051	0.424	0.021	0.120
	7x7	0.10	0.879	±0.002	0.012	0.083	0.684	0.017	0.103
	8x8	0.10	0.910	±0.002	0.025	0.307	0.947	0.013	0.095
	9x9	0.10	0.922	±0.001	0.029	0.206	0.990	0.010	0.090
Random lines	2	0.05	0.737	±0.004	0.000	0.000	0.016	0.035	0.137
	3	0.05	0.807	±0.003	0.000	0.001	0.088	0.025	0.118
	4	0.05	0.847	±0.003	0.001	0.006	0.275	0.020	0.106
	5	0.05	0.876	±0.002	0.000	0.022	0.441	0.016	0.101
	6	0.05	0.895	±0.002	0.000	0.050	0.537	0.014	0.094
	7	0.05	0.910	±0.001	0.008	0.042	0.785	0.012	0.091
	8	0.05	0.919	±0.001	0.000	0.124	0.860	0.011	0.088
	9	0.05	0.928	±0.001	0.001	0.107	0.897	0.010	0.086
Random lines	2	0.10	0.743	±0.004	0.000	0.004	0.107	0.035	0.136
	3	0.10	0.809	±0.003	0.003	0.009	0.313	0.025	0.119
	4	0.10	0.847	±0.002	0.005	0.933	0.581	0.020	0.107
	5	0.10	0.873	±0.002	0.004	0.080	0.747	0.016	0.100
	6	0.10	0.891	±0.002	0.000	0.158	0.826	0.014	0.094
	7	0.10	0.909	±0.002	0.031	0.189	0.972	0.012	0.090
	8	0.10	0.921	±0.001	0.000	0.420	0.989	0.011	0.086
	9	0.10	0.926	±0.001	0.004	0.433	0.997	0.010	0.085

[1]Low, medium, and high values represent 25th, 50th, and 75th percentiles of expected track numbers under each sampling design.

Layout, design, and typesetting by Vicki L. Webb

Photos by:

George Andrejko (Cover, pages iv, 30 [inset])
Norris Dodd (Pages 4, 5, 18)
Bob Miles (Pages vi, 6, 37, 45)
Dianna Van Sanford (Pages 16, 30, 40)